

XI. *New Bennettitean Cones from the British Cretaceous.*

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[PLATES 19–24.]

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BENNETTITES ALBIANUS, sp. nov.

INTRODUCTION.

This new species of *Bennettites*, the first petrified remains of the group to be found in the Gault of this country, is based on the structure of an ovulate cone. While it is true that only a portion of one cone is available, yet even this fragment includes hundreds of exquisitely preserved seeds which throw much new light on the structure of that most important group, the Bennettitales. Since the historic description so many years ago of the one and only specimen of the type of the group, *B. Gibsonianus* (see CARRUTHERS, 1870), no other well petrified cone has been found in this country,

and knowledge of the details of the fructifications of the group has been advanced chiefly by studies of the French *B. Morierei*, and a number of American forms. Beautiful as some of these are, the present specimen surpasses anything yet known in the Bennettitales for perfection of detailed preservation. Many points in the new species are novel, and on variations of less magnitude new fossil genera have been founded; but as in essentials the fruit conforms to the broad type "*Bennettites*," I prefer to use that widely known generic name for the new species.

The material from which the following description is compiled consists of a single fragment of a large ovulate cone. This was cut into as many sections as possible, but yielded only two longitudinal and seven transverse sections. Magnified by two diameters, five of this series of transverse sections are shown on Plate 19.

The specimen reached me in a small collection of "woods" from the Gault, which I had been examining in the course of my work of monographing the Cretaceous Flora for the Catalogue of the Geological Department of the British Museum. As I had been anxious to obtain a large number of specimens of "wood" from this horizon, I had got into touch with local collectors wherever possible, and among the most courteous and helpful was Mr. GEORGE C. WALTON, of Folkestone, who very kindly from time to time sent up specimens both from his own collection and from the Folkestone Museum, of which he is the Chairman. Some months ago, Mr. WALTON obtained some fresh specimens of "wood" from the Gault of Folkestone Warren, which he kindly sent up for examination. Among them was the present species. To Mr. WALTON I am therefore indebted for the specimen.

The longitudinally broken surface of the new *Bennettites* lying embedded in the matrix was so exactly like the ordinary, poorly preserved wood of that horizon that it was the merest chance that I did not overlook its true nature. Measurements were taken of what little could be seen of the cone structure, and then transverse and longitudinal sections exactly at right angles to them were cut. The longitudinal sections passed through the seed-stalks only, and did not include any seeds, but immense numbers of seeds were cut transversely in the transverse sections.*

Before the sections were cut, the broken edge of part of the specimen showed the long, very narrow seeds in relief; they were measured, and averaged 5–6 mm. in length, though the diameter was only 1–1·2 mm. The seed-shape is thus a contrast to the more globose seeds of the other species of the genus. Before cutting, the area of the specimen appeared to be 55 × 30 mm. in transverse diameter.

Regarding its presence in the Gault, it is to be noted that there is no previous record of *Bennettites* proper which has an unchallenged history from this horizon, and there is only one good record, *B. Morierei*, in which the evidence is at all strong.

* In ordinary cones of *Bennettites*, most transverse sections of the cones yield longitudinal or longitudinal-oblique sections of the seeds; but in this specimen the sections are all cut from near the flat top of a cone so immense that all the seeds are cut transversely (see p. 392 for details regarding the shape of the cone).

The Belgian *Cycadites Schachtii* is from the horizon, and is probably a member of the family, though it does not appear to be a *Bennettites* in the narrow sense.

The marked scarcity of the Bennettitalean plants, therefore, has hitherto been a salient character of the Gault, and one by which it is contrasted with the floras of the older Cretaceous and Jurassic rocks, containing numerous members of the family.

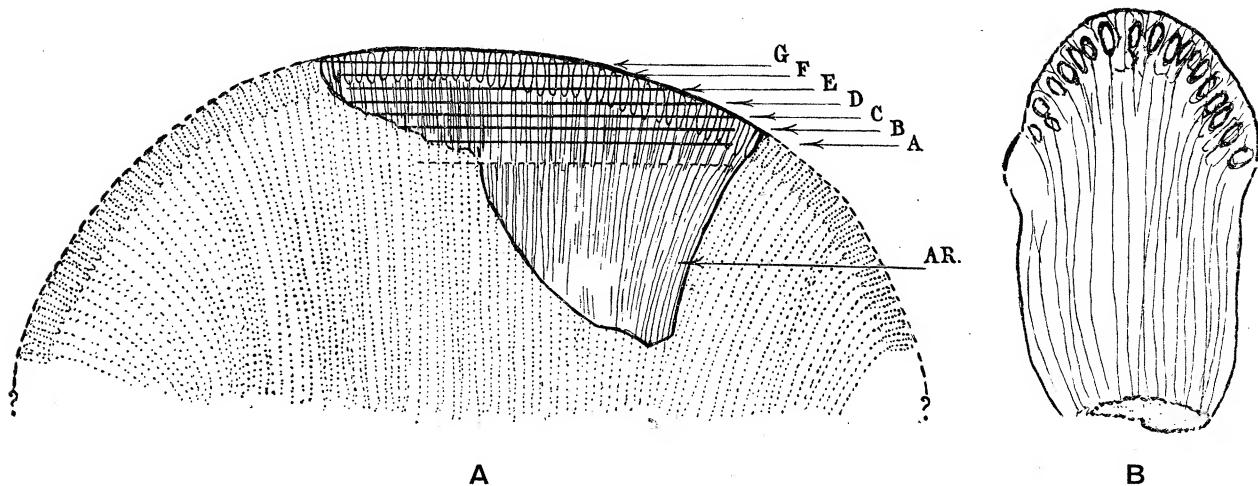
The beautiful *B. Morierei*, Sap. and Mar., which, when it was first found and for many years later, was always attributed to the Jurassic (Oxfordian), has recently (1910) been suspected by LIGNIER of coming from the Infra-cretaceous and probably from the Gault, because of the nature of its petrifying medium. While such a criterion must always be used with great caution, LIGNIER's knowledge of the peculiarities of petrifaction of other specimens of the horizons in question justifies him in concluding that the important *B. Morierei* is a Gault form. Judging solely by their structure, *B. Morierei* and the new species seem more closely allied to each other than they are to other known forms, though the likeness is not very close. It is interesting, therefore, to find that they are probably of the same geological age.

Of contemporaneous fossils of the same group practically nothing has been known in this country. Largely owing to their extremely friable nature, but few Gault plant remains of any sort are preserved. In various collections, however, a number of petrified specimens chiefly of "woods" are available. I believe that I have had nearly all the Gault fossil plants in the country through my hands, and this is the only remains of a member of the Bennettitales I have seen among them. Though that may enhance the interest of the specimen, it must not lead to the conclusion that these plants were actually rare in Britain in Gault times. About that no data are available yet. We do know, however, that the group was rapidly approaching extinction, if it was not already extinct, over the greater part of the globe, and hence it is extraordinarily interesting to find a species growing at that time which produced by far the largest and most elaborate cone on record in the family. It is obvious and tempting to compare this with the giant and elaborate forms which appear in so many groups of animals shortly before their final extinction: but palaeobotany is so far behind animal palaeontology in a detailed knowledge of the fundamental criteria to be used in interpreting its fossil forms, that we do not know whether it is legitimate or not to compare giant *fructifications* with the giant vegetative organs of animals. There is nothing to show that the new species was of large vegetative habit. More detailed knowledge is needed before we can determine such interesting points about these plants.

DESCRIPTION OF THE SPECIMEN.

The portion of the cone which we have, was but a part of a rather flat, dome-shaped, presumably symmetrical structure. Before cutting the segment was 55 × 30 mm. in area, but some was lost in cutting and grinding. Text-fig. 1 shows a

diagram of the part which was preserved, the direction of the sections cut, and a suggestion of the total size and shape of the cone when complete.

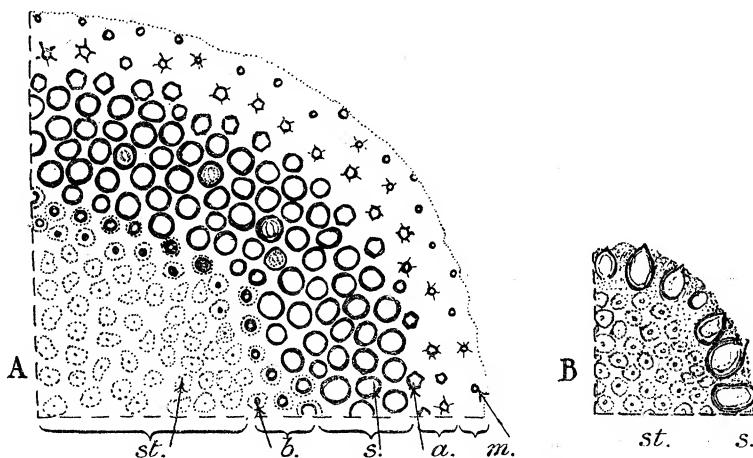


TEXT-FIG. 1.—A comparison of the arrangement of the ovulate cones in the new species and in *B. Morierei*, both natural size. A, *B. albianus* sp. nov. The part filled in with unbroken lines represents the part of the cone preserved in the specimen, the dotted lines indicate the probable extension of the actual cone. Lines A to G represent the series of transverse sections, and area AR the longitudinal sections on which the restoration is based. B, *B. Morierei*. View of the cone taken from LIGNIER'S description (1894).

Judging from the ordinary type of *Bennettites* cone the fact that the seeds are all cut transversely would make it appear as though the sections must have been cut tangentially to the surface of the cone, but the longitudinal sections of the stalks show the impossibility of this. Taking into consideration all the structures revealed by the sections, it is clear that the transverse series is really transverse to the cone. As the stalks were all running nearly vertical and the seeds all standing upright, we must be dealing with the top of the cone, which, as WIELAND (1906) showed, is the only place where the seed-stalks are vertical and the seeds upright. WIELAND mentions that the cones of the group are "egg-shaped" and the lateral seed-stalks curve outwards, carrying the seeds at an angle. As the arrangement of seeds, stalks and inter-seminal scales is identical in the present new species with that found in other members of the group, one must assume in it also the existence of a symmetrical cone built on a broadly similar plan. In that case, the minimum size it must have had to allow for the structures preserved in the sections we have, must have been 70 mm. in diameter, and, as will be seen from the diagram in text-fig. 1A, the natural "egg-shaped" curve leads to a cone of at least 120 mm. in diameter, an immense contrast even to its nearest ally *B. Morierei*, a sketch of which, also natural size, is given in the same text-fig. 1B. I incline to the belief that the new cone may have been flatter and more cushion-like, though there is nothing in its structures, so far as we know them, to render it impossible for the cone to have been nearly spherical or egg-shaped. The diagram does not indicate such a shape, but the reader can easily

deduce the size of it from the part shown if he inclines to the belief that it was shaped like the other members of the family. According to either interpretation the new cone is very much larger than any other known *Bennettites*. The ovulate cone of *B. Gibsonianus* is little over 20 mm. in diameter, and WIELAND, describing the most important American form, *B. Wielandi*, says (1906, p. 109), "The greatest strobilar diameter, which is somewhat distal, is from 2 to 2·5 cm. exclusive of the covering of bracts."

That the portion preserved (which is indicated by unbroken lines in text-fig. 1A) was from the apex of the cone is evident from the following facts: the upper sections, G and F, contain seeds only (see figs. 4 and 5, Plate 19), while the basal section A contains nothing but stalks with a few seeds on one side (fig. 1, Plate 19), and these stalks are cut in true transverse direction, at right angles to those in section AR, in which they are cut longitudinally; in the transverse sections the inner seeds are cut near their bases (see zone *b*, text-fig. 2A, and Plate 19, figs. 2, 3 and 4) and the outer seeds are cut through their apices (see zone *a*, text-fig. 2, and Plate 19, figs. 3 and 4). As WIELAND (1906) pointed out, the seeds only stand vertically at the top of the cones, the stalks below that bending so as to give a slightly oblique and, still lower down, a true longitudinal section of the seed in transverse section of the cone. In all the sections A to G all the seeds are cut in dead-true transverse sections, or in transverse sections with a minute obliquity.



TEXT-FIG. 2.—Comparison of transverse sections of the cones of the new species and of *B. Gibsonianus*, both \times about 2 diameters. A, *B. albianus* sp. nov. Transverse section of cone showing the central stalk region *st.*; the bases of seeds *b.*; seeds at various levels in transverse section *s.*; the apices of seeds in transverse section *a.*; and the seed micropyles between the terminations of the intersepaline scales *m.* B, *B. Gibsonianus*. Corresponding transverse section showing only stalk region *st.*; and seeds in oblique and longitudinal sections *s.*

The immense number of the seeds and their small size will be apparent on examining and counting them in figs. 2-5, on Plate 19, but as the smaller bases, apices and micropyles are not visible in these photographs, text-fig. 2 should be referred to. In

section E (fig. 3, Plate 19) there are over 250 seeds. As can be deduced from this photograph, this section covers not very much more than one-fourth of the total area of a transverse section of the cone, assuming, as is rational to assume, that the complete transverse section of the cone was circular. In text-fig. 2A, an exact fourth part of such a section of a cone is drawn, and it contains 150 seeds. It appears, therefore, that 600 or more seeds were present in a single transverse cut through the cone. As each seed appears to be cut only twice or three times in the series, it is clear that, even if the cone was a flat, cushion-like structure, and not egg-shaped like the rest of the genus, yet its total number of seeds must have run into thousands. This is a great contrast to *B. Gibsonianus* and other species, as is shown by the sector of a corresponding section of *B. Gibsonianus* in text-fig. 2B.

DETAILED DESCRIPTION.

The *axis* of the cone is not present, so that there is nothing to indicate exactly what it was like. It seems clear that it cannot have had the almost pointed, conical shape illustrated in so many of WIELAND's descriptions, because such an axis could not have supported so large an area of upright seeds (as it must have done in the present instance) without the whole cone having been huge beyond belief. It is likely, therefore, that the cone axis was rather flat, probably more flat and cushion-like, as well as much bigger, than that in *B. Gibsonianus*.

Of the outer *bracts* no portions remain. The cone was evidently ripe, and having such a hard, compact pericarp, it may very well have been naturally denuded of the bracts.

The Interseminal Scales.—The stalks of these scales are small in diameter, averaging about 0·2 to 0·4 mm., and of very irregular outline. As in *B. Gibsonianus* and other described species, their irregularities are closely interlocked around the seed stalks, in the region of which they form a mass of closely adpressed organs. In the lowest section (A) about seven interseminal scales on an average surround each seed stalk. In this region, some distance from the seed, their tissues are comparatively thin-walled, but they rapidly become more sclerised nearer the seed region, and terminally are formed of excessively thickened stone cells. There is in each scale, with few exceptions, only a single strand of markedly smaller elements, presumably vascular. I cannot distinguish definitely oriented xylem and phloem such as is described by both LIGNIER and WIELAND, though the preservation in the new species is perfect; the actual differentiation of the vascular bundle seems to have been less than that in some of the other species. At the same time it is distinguished from the other known species by the presence of large and well-marked resin passages, associated with the strands. In a few of these there seem to be traces of a definite orientation, and some indication of a doubling of the strand such as is described by LIGNIER (1904), but this is infrequent in comparison with the great number where the

strand is obviously only a mere group of small elements, all alike save for one or two, irregularly placed, with thinner walls.

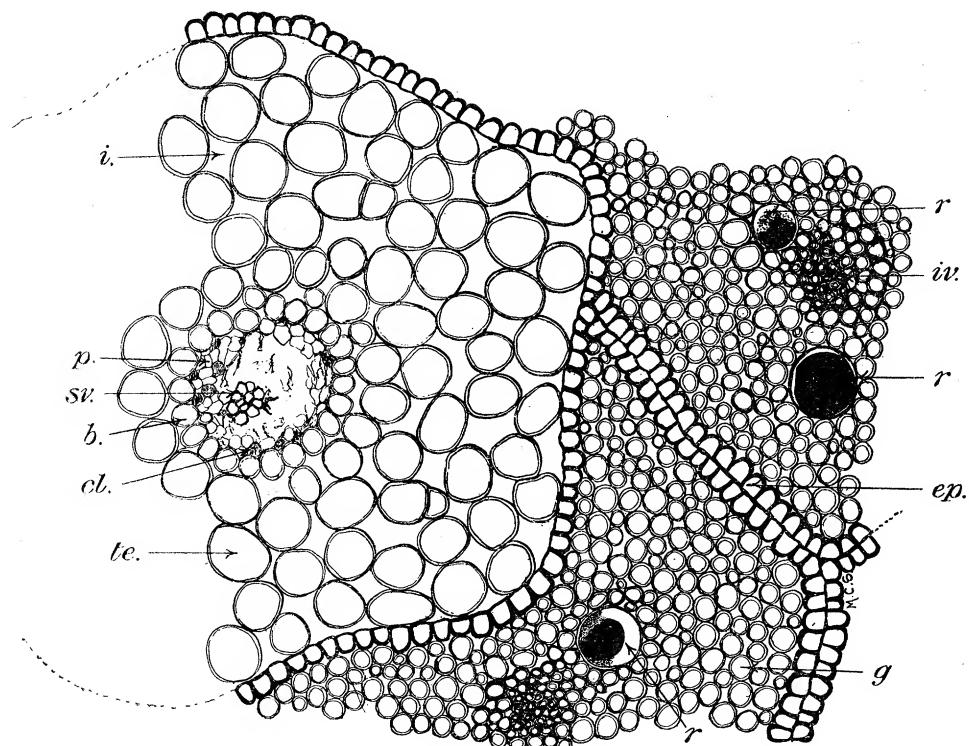
Those parts of the scales on a level with the tops of the seeds, and in particular those round the apices of the seeds, were terminally expanded, as were the scales in all known species of the group, but these terminal expansions were more completely fused in certain regions than is described for other species (see p. 399 and text-fig. 6). Beyond the region of fusion the scales separated and rounded off, and were externally covered by a very peculiar and characteristic layer (see p. 397). This peculiar zone of cells (a modified epidermis) not only rounded off the interseminal scales but encircled and was united to the micropyle, running down the outside of its throat for some distance and dying out in five-rayed arms which seem to correspond both to the ribs of the seeds and to the separation of the interseminal scales, though lower down the interseminal scales get somewhat dislodged, so that no longer do their limiting layers tally with the corners of the seed ribs.

Details of the Tissues of the Interseminal Scales.

The Epidermis.—Considering this from below, *i.e.*, from the point nearest its attachment level, upwards : near the attachment of the scales the epidermal cells are not always quite easy to recognise, as they are there much like the ground-tissue cells of the scale, but very soon they become a well-marked compact layer of rather small cells with definitely thickened walls, averaging about 12–15 μ in diameter (see text-fig. 3). In sections cut somewhat higher up, *i.e.*, nearer the region of seed attachment, the epidermis of the scales becomes more conspicuous (see text-fig. 4) because, though the actual size of the cells remains about the same, their size relative to the adjacent tissue is greatly decreased owing to the enlargement of the other elements of the scale-tissue. Text-figs. 3 and 4, *ep.*, should be compared. The walls of this layer are generally thickened so that the centrifugal and radial walls are thicker than the tangential.

This limiting layer is lost in the region where the scales are mutually fused, and also fused with the seeds (*cf.* text-fig. 6, p. 399). Whether it is to be looked upon as the same layer as that very definite epidermis of a totally different type which bounds the exposed portions of the scales I do not know, but as both seem to be true outermost limiting layers, presumably they are differing modifications of the same fundamental epidermis.

The *external epidermis*, *i.e.*, that limiting the exposed portions of the scales, which I provisionally call the *plastid layer*, is to be seen wherever the surfaces of the scales are cut. It is drawn accurately as it appears on the border between two adjacent scales in text-fig. 5, where the layer a^1 belongs to one scale and the layer a^2 to its neighbour. The cells here are radially elongated and oblong, with extremely delicate walls where adjacent to each other. They are closely and regularly packed, and cover the whole outer surface of the scales, sometimes

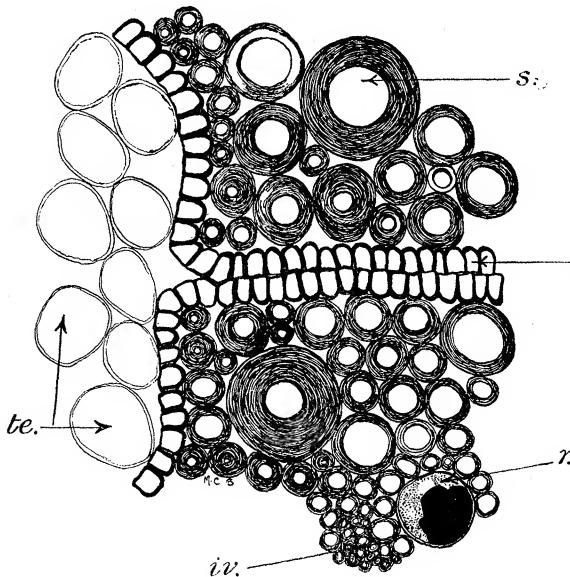


TEXT-FIG. 3.—*B. albianus* sp. nov. Transverse section of seed-stalk and part of two surrounding interseminal scales, from low down in the series. [Slide F.] In seed-stalk: *te*, tubular epidermal cells with *i*, many intercellular spaces; *b*, cortex, which appears to function as bundle sheath; *sv*, xylem of vascular strand; *p*, parenchyma and phloem; *cl*, a few cells with coloured contents, equivalents (?) of LIGNIER'S "assise colorée." In interseminal scales: *ep*, epidermis; *g*, ground tissue; *iv*, vascular strand; *r*, resin canals associated with vascular strand.

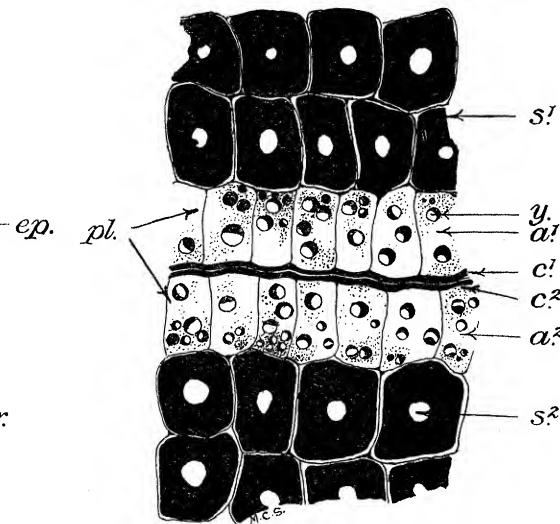
apparently in two or more layers, but this, I think, is due to the rapid curve of the scales which they cover. In most places they are seen to form a single layer surrounding each scale (see fig. 1, Plate 20; fig. 16, Plate 21; and text-figs. 11 and 17).

The cells of this layer are about $15-20 \times 30-40 \mu$ in diameter, and all their walls appear thin save their outward wall. This is covered by a very thick and well pronounced cuticle (see *c*, text-figs. 5 and 11). The cuticle, which can be seen in many places bounding the limits of adjacent scales, as in text-fig. 11, *c*, is preserved as a noticeably brilliant band, a clear ruddy orange in colour. It reminds one forcibly of the similar brilliant cuticles in parts of recent Cycadean fructifications. The cells are noticeable in containing numerous spherical granules or globules (see *y*, text-fig. 5), which are distinctive in appearance. They appear to me to be exactly what the carotin granules which replace the chlorophyll in the outer layers of maturing Cycad seeds would look like if petrified, and suggest the probability that, in the early stages of development, this epidermal layer was chlorophyll-containing and assimilative, and that, later, just as in living Cycads, its green grains changed to vivid carotin, which, coupled with the strong and coloured cuticle, coloured the whole fructification orange or reddish. It has been suggested to me that these bodies

were mucilage drops, but I have seen much mucilage and resin fossilised in *Bennettites* and other forms, but none of it looked quite like this. While the above plastid theory of the structures is not open to proof, I make the suggestion with some confidence in its probability.



TEXT-FIG. 4.



TEXT-FIG. 5.

TEXT-FIG. 4.—*B. albianus* sp. nov. Part of seed stalk and surrounding interseminal scales, from a higher level than text-fig. 3. *te.*, epidermis of seed-stalks; *ep.*, epidermis of interseminal scales; *s.*, large stone cells of ground tissue of scales; *iv.*, vascular strand; *r.*, resin canal.

TEXT-FIG. 5.—*B. albianus* sp. nov. The edges of the terminal parts of two adjacent interseminal scales. *pl.*, the bounding layer, or "plastid-epidermal" layer covering each, containing plastids *y*; *s¹*, stone cells of the scale; *a¹*, plastid layer of the same scale, with its cuticle *c¹*; *c²*, cuticle; *a²*, plastid layer; *s²*, stone cells of neighbouring scale.

The relation of this plastid layer to the seeds is a curious one, and must be considered. For some distance up the micropyle, but not so far as to reach its external opening, the layer is not only closely adpressed, but actually adherent, its cells following the outline of the micropylar cells (see text-fig. 11). Text-fig. 11 is drawn just a little below the terminal freedom of the scales, where they, too, are already partly fused, as can be seen at *fpl.*, where the layers are united and not separated by a cuticle.

Lower down this layer vanishes gradually, as the cells merge with the thickened stone cells of the interseminal scales. Stages of the passage of the layer into the stone cells can be seen in various sections; first, the layer begins to have its walls somewhat thickened, but retains the plastids, then, as the shape of the cells becomes more rounded and like the stony layers, and their cell-walls become increasingly thickened and pitted, the plastids are fewer, until possibly only one or two remain in a very thick-walled cell, which is the last to be recognisable in the transition series.

In the region where the scales are all mutually fused (see text-fig. 6 and text-fig. 14, F), this plastid-epidermal layer loses its identity completely, as does the epidermis coming up from the lower end of the scales.

NATHORST (1909, Plate 6, figs. 4, 9, etc.) figures interseminal scales from semi-petrified "impressions" of *Wielandia*, which show a blackened border delimiting the individual scales. It is suggestive to compare these with the present species (see Plate 21, fig. 16), though NATHORST's material, naturally, does not show the minuter details visible in the present specimen. Is it not probable that his layer also was a contents-containing epidermis, presumably with a part to play similar to that of the plastid layer just described?

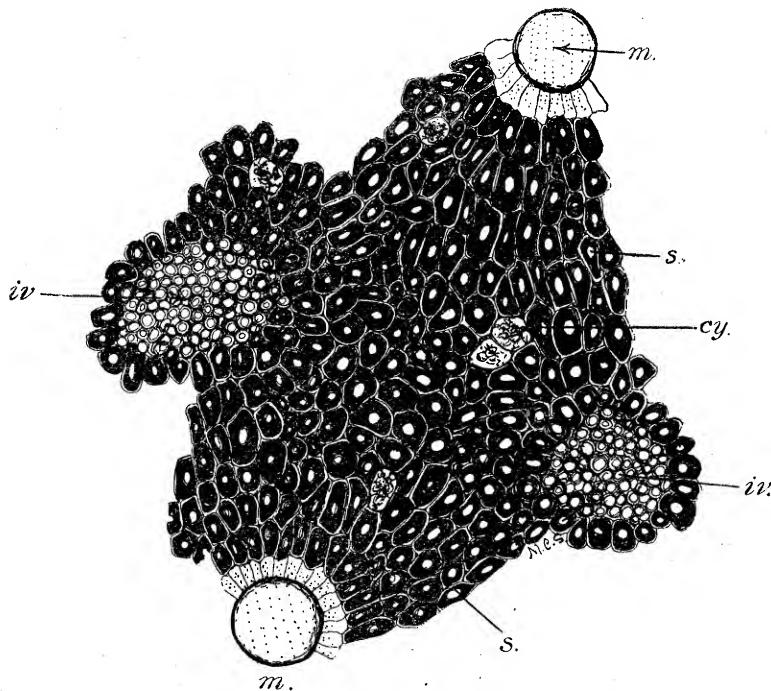
The *vascular strands* of the scales run as nearly centrally in each scale as their very irregular shape allows. There is but a single, unbranching strand in each, which dies out near its free end. At the lowest level cut by the transverse sections, the strands consist of about 15–30 very small thick-walled elements (averaging 8–12 μ in diameter), with which are one or two thinner-walled elements of about the same size. They are all packed closely together, fitting in with almost no intercellular spaces. So far as I can judge, they seem to be devoid of any limiting layer or any definite orientation. At this comparatively low level of the scale they stand out as thicker- and darker-walled than the surrounding ground-tissue cells of the scale (see text-fig. 3, iv., and Plate 22, fig. 1). But further up, where the scales become packed with large stone cells, they are conspicuous as relatively lighter coloured and thinner-walled than the surrounding tissue, though their actual size has increased on an average to 12–25 μ in diameter, and their walls are somewhat thicker than they were lower down. Text-figs. 3 and 4 should be compared. At the upper end of the scales the strands have increased in area considerably, and are conspicuous light patches in the middle of the mass of strongly sclerised tissue (see iv., text-fig. 6; Plate 21, fig. 18).

I am not able to distinguish the markings of differentiated xylem and phloem, either in transverse or longitudinal sections. The strands of the species described by LIGNIER and WIELAND (who both speak confidently of the orientation of the xylem and the phloem) are apparently more highly differentiated than in the present instance.

Resin Cells.—Until near the termination, all through the length of each interseminal scale there runs one, or often two, and sometimes three, conspicuous resin cells. They tend to run alongside of the vascular strand, as is to be seen in text-figs. 3 and 4, and Plate 22, fig. 1, at r. They are more conspicuous in the lower regions of the scales, because there the general ground-tissue cells are smaller, as will be recognised on comparing text-figs. 3 and 4.

These resin passages are definitely surrounded by a cell-wall, appearing to be, in fact, single cells. Each of these cells is circular, and averages from 50–80 and more μ in diameter. They are generally partly or completely plugged by conspicuous black masses of "resinous" material.

Though large irregularly running "mucilage canals" are, of course, common in the pith, petioles, etc., of all previously described species, such definite cells as those described above, associated with the vascular strands of the interseminal scales, have not, so far as I am aware, been described in any other species of *Bennettites*. LIGNIER points out that there are no gum canals in the interseminal scales of *B. Morierei*.



TEXT-FIG. 6.—*B. albianus* sp. nov. Showing the complete fusion of adjacent scales round seed apices.
m, micropyles of seeds filled in diagrammatically; *s.*, stone cells of scales drawn to detail; *iv*, vascular strands of interseminal scales (one to each); *cy*, crystal-containing or secretory cells scattered in stone tissues of scales.

Towards the end of the scales these cells die out. There are in these regions, and right through to the surface of the scales, isolated single cells of a different type, not tubular, but in shape and size like the stone cells among which they lie, which may be muclaginous or resinous, but which are very different in appearance and distribution from the cells now considered (see below, pp. 400 and 405).

The general *ground-tissue* of the scales, low down, consists of generally uniform, small rounded cells, averaging $10-20\ \mu$ in diameter. Their walls are somewhat thickened, and are very definitely rounded off, so as to leave considerable intercellular spaces (see text-fig. 3, *g*).

From still lower regions of the scale, approaching its level of attachment to the peduncle, LIGNIER describes a central, soft, parenchymatous ground-tissue for the scales, coupled with a general increase of sclerification in an upward direction. The fact that the lowest level reached by the scales in the fragment of the new species is still considerably sclerised, and not yet provided with a parenchymatous centre,

lends its quota of support to the suggested magnitude of the cone, as given in text-fig. 1.

The *stone* cells, which invade and gradually replace the whole of the ground-tissue, are very various in size, some of them being $90\ \mu$ and more in diameter, others only $15\ \mu$. At the base of the expanding portion of the scale (see text-fig. 4 and fig. 17, Plate 21) they are nearly all round in outline whatever their size, and thus have between them considerable intercellular spaces. But further up, and particularly where the scales lose their identity and completely merge, the stone cells are closely packed together, and become more uniform in size and are variously shaped (see text-figs. 5 and 6). Here their walls are much thicker, so that the cell lumen is very small, and, in some cases, almost obliterated. These cells can be seen forming the ground-mass in photographs (figs. 16 and 18, Plate 21, and fig. 4, Plate 22).

This excessive hardening of the interseminal scale tissues, coupled with their complete fusion, as is seen in fig. 18, Plate 21, and text-fig. 6, must have produced an extremely hard, woody "fruit," with an unbroken shell of great resistant power.

In the ground-tissue of the terminal portions of the scales, scattered among the stone cells are isolated cells with thin walls and queer twisted dark contents. The appearance of the cells is very suggestive of crystal-containing cysts: while it is, of course, possible that they were mucilaginous. They are to be seen at *cy* in text-fig. 6, text-fig. 11, and Photo. 4, Plate 22. A few entirely similar cells are found in the conspicuous stone-layer of the seed (see p. 404).

THE SEED STALKS.

In the material available, the seed stalks run nearly straight for over 30 mm., and as the peduncle attachment is not preserved, it is impossible to estimate how much longer they may have been. They must have extended for some considerable further distance, judging by the general contours of the cone, and also by the fact that they have no indication of any change in their character such as is described by LIGNIER for the bases of the stalks. Each seed stalk is characterised by having a small central strand and a massive, loosely packed surrounding tissue, as is common in the genus. As was made clear by LIGNIER (1894) the stalks have no single limiting layer outside this false cortex, but are bounded by the epidermis of adjacent interseminal scales.

LIGNIER described those of *B. Morierei* in great detail, and as the general characters of the stalks of the species are so similar, one may accept his interpretation of the cortex-like layer as being really a multicellular and lacunar *epidermis*, a deduction he made from his study of aborted seeds. The character of the cells in the present species is seen in Plate 22, fig. 2.

A detailed drawing of a typical seed stalk at some distance from the seed is shown in text-fig. 3, where the relatively large size of this mass of "tubular"

epidermal cells is apparent. At this region the cells average about $50\ \mu$ in diameter, and are the same size as in LIGNIER's specimen. They are well rounded, stand away from each other firmly, and have walls which were apparently somewhat thickened, but there is no means of knowing the nature of the thickening.

The total lack of tracheal elements in the seed integuments, and the very minute size of the elements in the stalks and interseminal scales, suggest that possibly this capillary layer of spongy tissue in the stalk acted as do the cells in a sphagnum leaf, and drew up and held water in reserve for the needs of the seeds and embryo. This water would be prevented from evaporation by the aperture-less, coherent "shell." While this idea is put forward as a mere suggestion, it seems to me more convincing than LIGNIER's idea that this unusual layer was developed to reduce the friction with the neighbouring growing parts; were any protection against the friction of growth necessary, such special layer would have been developed in every fruit. But the absence of all vascular tissues in such complex gymnospermic seeds is remarkable, and my idea accounts for both the peculiarities of the stalk and the seed.

Within this very unusual epidermis lies a single more regular layer of rather smaller cells (*b* in text-fig. 3). Morphologically this must represent a cortex, but physiologically it may perhaps have performed the functions of a bundle sheath.

WIELAND (1906, text-fig. 61) draws this layer of cells with walls thickened like those of the epidermis of the interseminal scales, but that is not how they appear in the present species. Within this is very irregularly present a layer with a colouring matter in the cells, but more often the layer is present, and the cells are *not* coloured, see *cl.*, text-fig. 3. It appears possible that this represents the same layer as that described by LIGNIER (1894) as his *assise colorée*.

Within this layer is a mass of 100 or more small cells, forming the vascular bundle. There is a small group of about a dozen tracheids, *sv.*, surrounded by parenchyma *p*, text-fig. 3, with which are some granulated or darker cells very suggestive of the sieve tubes of a normal phloem. In longitudinal section I can only find one place in which the characteristic xylem wall thickening is apparent, and in this a group of three elements have very delicate spiral-reticulate thickening bands.

Approaching the seed, the seed stalks become cup-shaped, and the base of the seed is surrounded by a cupule or aril-like termination of the stalk. This interesting and peculiar feature is illustrated in the restoration shown in text-fig. 13, though in order to show the seed in position a number of the outer "cupule" cells are imagined to have been torn off. These cells surrounding the seeds are illustrated in photos, fig. 10, Plate 20; figs. 11, 12 and 13, Plate 21, *t*, and in diagrams, text-figs. 13 and 14. On a larger scale they are seen in photo 8, Plate 19, and text-figs. 7 and 8. The base of the seed is embedded in a multicellular aril-like cup of these cells, but further up it is reduced to a single layer which follows the seed closely for the whole of its length, as far as the apical ribs, though it becomes inconspicuous owing to the reduction of the size of the tubular cells.

In the region of the base of the seed the large size of these cells makes them very conspicuous, and they are sharply contrasted to the other tissues amid which they lie. In nearly all individuals, by the middle of the seed, they cease to be so much in evidence, but they run up, like fine hairs, in the space between the interseminal scales and the seed-integument, see text-figs. 8 and 10, *t*. The constriction of the seed stalks just below the seed attachment, which WIELAND describes as being so marked, is barely present, but instead the *enlarged* tubular cells form this sheath round the seed. As this layer reaches the seed-base region it shows a very noticeable increase in the size of the diameter of the individual cells, which can be seen on comparing this layer in the photographs shown on Plate 21, figs. 11, 12 and 13, with the same layer in figs. 14 and 15, which are taken from stalks at some distance below the seed. These photos are all on an identical scale of magnification. This curious and interesting enlargement and then terminal hair-like reduction of the tubular-epidermal cells of the stalk is established by many measurements as being the normal thing in this species. In *B. Morierei* also LIGNIER noticed an increase in the diameter of the cells of this layer toward the seed region, and a reduction in their diameter at the base of the stalks, though he does not seem to have recognised in his species such a definite and peculiar seed-covering as is present in the new species.

Within this layer, apparently also derived from the stalk, is a layer or two of irregular, squarish, thin-walled cells which are very liable to break down, particularly in the middle of the seed, and to leave a space between it and the "cupule" of hairs. Their most general state of preservation is to be seen at *ud*, text-fig. 8. This layer must represent that which WIELAND (1911) calls the "blow-off" of outer flesh, homologising it with OLIVER's (OLIVER and SALISBURY (1911)) "blow-off" in the Palaeozoic seeds.

With structures so peculiar as the whole complex seed arrangement in the present species, I hesitate very much to assume such homologies, and will therefore call the layer in my stalk-extensions the deliquescent layer. The crushed cells of this layer can usually be detected round the seeds if sought for, often present as shown at *d*, text-fig. 8. Toward the apex of the seed, approaching the region where scales and seeds are all adherent, the layer is better preserved, and its irregular double or treble nature can be well seen at *d*, text-fig. 9. This is taken from a level just below the complete fusion of the scales, but where their epidermal layer has not yet become distinct. Notice the irregular contours of the edges of the scales, and the way the cells are interlocked with the deliquescent layer.

THE SEEDS.

As in other species of the genus, the seeds are borne singly and terminally on the seed-stalks. They are orthotropous, and each stands embedded in the deep goblet-

like extension of the end of the seed-stalk just described. The seeds are more elongated and slender, and also much smaller in diameter than those of *B. Gibsonianus* and other species. *B. Morierei*, which is the likest to the new species, has a diameter of 2·5–3 mm., while the seeds now described average 1·2 mm. at their greatest diameter. The new species differs from the others in having five definite ribs at the apex of the seed, a number which is often increased to six. *B. Morierei* has four ridges, and occasionally five.

Below the apical ridges the seed is roughly circular and smooth, with a rather pointed base. Its general shape is torpedo-like. A series of transverse diagrams from various levels is given in text-fig. 12, p. 411, which, considered in conjunction with text-figs. 10 and 14, should make its shape clear.

As is to be seen in the series of photographs in Plate 19, figs. 1–5, the seeds are very closely packed, and their circular outlines are somewhat irregularly compressed in relation to each other.

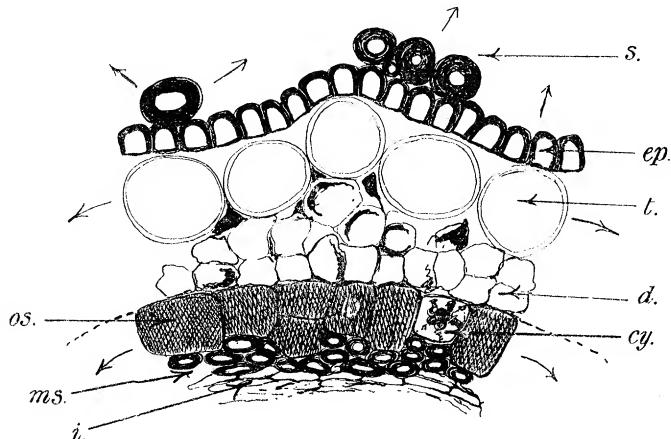
Their apices are not only tightly surrounded by, but are completely adherent to, the region of the fused scales (see text-figs. 6 and 11, and Plate 21, fig. 18). It is very difficult to determine the comparative morphology of all the many layers composing the seed and its various coverings. Eleven distinct sets of cells go to the making of the integumentary coverings alone, if the two layers of the extensions of the stalk be included as seed coverings, as seems only reasonable from their cupule-like nature; but, on the other hand, these two do not form part of the seed integument in a stricter sense. In the following description I will not again refer to these layers, which have been dealt with under the heading of seed-stalk tissues.

Details of the Seed-Structure.

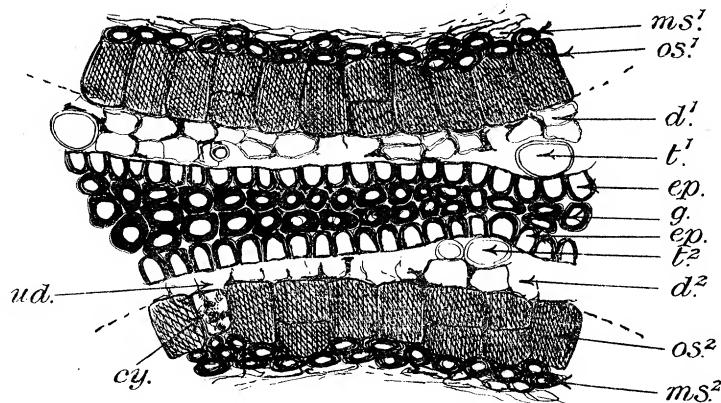
The definite, hard integument of the seed proper, the major length of which appears generally to be separated by a space from the hair-like cupule and the interseminal scales by the breakdown of the "deliquescent layer" of the stalk extension (see text-fig. 10), reveals in transverse section that it is composed of three layers, viz., the outer stony or limiting layer, a middle stony or fibrous layer, and an inner thin-walled layer.

The *outer stony layer* consists generally of a single or a partly double layer of large, squarish cells, which average about $30 \times 45 \mu$ to $40 \times 50 \mu$. These fit together in close rank, and form a regular shell. Where two cells are in radial sequence they fill together approximately the same space in a radial direction as their one neighbour. The cells are oriented at approximate right angles to the main axis of the seed, and as their walls are very thick, in transverse sections of the seed, the walls are generally cut tangentially, and so the cells look solid, and lumina are seldom apparent. This can be seen in the photographs on Plate 21, fig. 17, and Plate 19, figs. 7 and 8, and text-figs. 7, 8, 9, and 10, os. This fact affords the explanation of LIGNIER's interpretation of this layer in *B. Morierei* as being "fleshy," for in his

specimen the less perfectly preserved walls, when cut tangentially through their thickness, as they would be in both transverse and longitudinal sections of the seed,



TEXT-FIG. 7.—*B. albianus* sp. nov. Small part of the seed coverings from the lower half of a seed. *i.*, inner, thin walled tissue; *ms.*, middle stone or fibrous layer; *os.*, outer stone layer; *d.*, deliquescent layer of surrounding stalk tissues; *t.*, tubular cells of stalk "cupule"; *ep.*, epidermis of adjacent interseminal scales; *s.*, stone cells of adjacent interseminal scales.

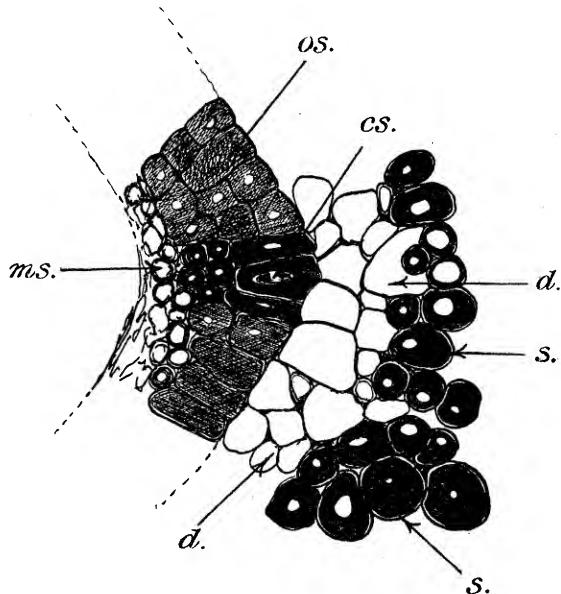


TEXT-FIG. 8.—*B. albianus* sp. nov. Portions of two neighbouring seeds from above the middle. *ms*¹, middle stone or fibrous layer of one seed; *os*¹, outer stone of one seed; *d*, deliquescent layer of one seed; *t*, tubular cupule of one seed; *ep.*, epidermis of intervening interseminal scale; *g.*, ground tissue of intervening interseminal scale; *t*², tubular cupule of neighbouring seed; *d*², deliquescent layer of neighbouring seed; *os*², outer stone of neighbouring seed; *ms*², middle stone or fibrous layer of neighbouring seed; *ud.*, usual state of complete breakdown of deliquescent layer; *cy.*, crystal-containing or secretory cells in stone of seed.

have a deceptive appearance, as though they were thin-walled elements filled with a brownish mass.

The corner stone cells of the seed in the present species are quite noticeably darker walled, and stand out from the rest of the testa (see photographs in Plate 20, fig. 6; Plate 21, fig. 17; Plate 22, fig. 4; and in text-figs. 9 and 10, *cs.*). These elements are cut in transverse section, showing their lumina clearly, and appear to run in the seed

longitudinally. In several of the seeds they tend to split apart, so that the apex shows five cracks, one through the centre of each corner (see Plate 20, fig. 5).



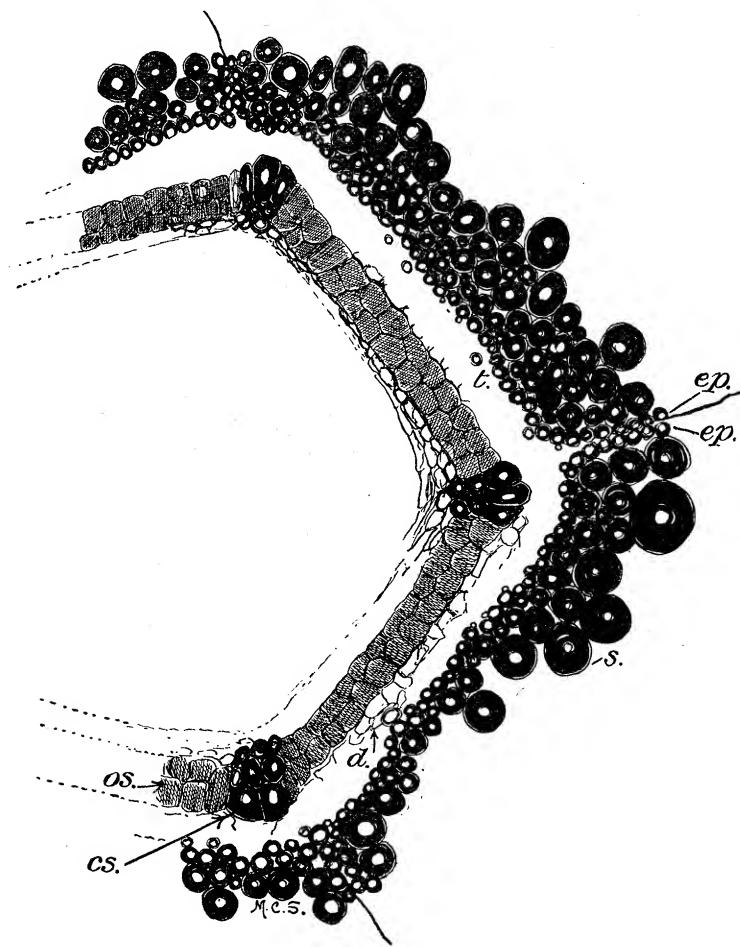
TEXT-FIG. 9.—*B. albianus* sp. nov. Corner of one of the five-ribbed apices of seed. *ms.*, middle stony or fibrous layer; *os.*, outer stony; *cs.*, stone cells of corner; *d.*, "deliquescent layer": note the irregular size of the cells and the way they fit round the irregular edge of the interseminal scales; *s.*, scale cells.

The *middle stony or fibrous layer* consists of a varying number, 1–4 rows, of much smaller stony fibres, each rounded or oval in section, and averaging 10–15 μ in diameter. Their cell walls are considerably thickened, but lumina equal to or greater than the thickness of the walls are left (see photographs in Plate 19, figs. 7 and 8, and text-figs. 7 and 8, *ms.*). These fibres run vertically, and appear to be considerably elongated, though it is not possible to determine their exact length. They are freely pitted.

The *inner, thin-walled layer* consists of two or three rows of thin-walled cells, generally somewhat crushed and rather irregular, but arranged so that their flattened outlines fit closely together. This layer can be seen clearly in photographs 7 and 8, Plate 19, and in text-fig. 7, *i.* In many of the seeds it is represented by a fibrous black line of crushed cells.

Oil, or crystal-containing (?) cells are to be seen here and there, sparsely scattered in the surface layer of the seed. A few occur near the seed bases, but they are more frequent near the apices. The cells are isolated, and replace single cells of the outer stony layer, see text-fig. 8, *cy.* They approximate to the size and shape of the adjacent stone cells, but have thin walls, and a large lumina in which are irregularly twisted contents, sometimes spikes from which appear to be attached to various places on the wall.

Towards the apex of the seed, where the seed testa and the interseminal scales all merge their tissues, exactly similar cells are found both isolated and in clusters, replacing the stone cells of the scales. Here, too, they are conspicuous by reason of the contrast between the dark mass of the thick-walled stone cells in which they lie,



TEXT-FIG. 10.—*B. albianus* sp. nov. Transverse section of ribbed portion of seed, showing three of the five ribs, and the space between the seed and the surrounding scales left by the breakdown of the deliquescent layer and reduction of tubular cupule to hair-like terminations of the cells. At this level the interseminal scales are just beginning to differentiate their limiting layers. *os*, stone of seed; *cs*, stone cells of corners, cf. Plate 21, fig. 17; *d*, remains of deliquescent layer; *t*, tubular cells of cupule; *s*, stone cells of ground tissue of interseminal scales; *ep*, epidermis of same.

and their clear white but partially filled lumina. That they were crystalline or glandular cells of some kind seems certain.

The *vascular supply* of the seed seems to consist solely of the single very small strand which runs up from the stalk and just enters the base of the testa, passing straight through it, and dying out in the nucellus, apparently without even the few basal branches described for *B. Morierei* and other species of the genus (see text-fig. 14). The strand can be seen passing into the base of the testa in a photograph

of a very slightly oblique transverse section on Plate 21, fig. 12. The xylem elements are small and are finely reticulate-scalariform.

Throughout the whole of the rest of the seed there appear to be neither vascular strands nor isolated tracheids. (There are, of course, strands in the embryo itself, which will be dealt with later.)

The *micropyle*, which is so conspicuous a feature of Bennettitalean seeds, is well seen in a large number of places. It forms a distinct circular tube with a complex multicellular wall in which three quite distinct layers are distinguishable. The micropyle can be seen, but not very clearly, in the photograph Plate 20, fig. 2. Plate 21, fig. 18, shows a photograph of the junction of the micropyle proper with the top of the seed proper, but the character of the free micropyle can perhaps best be seen in the photograph on Plate 22, fig. 3. There the inner, limiting layer is very conspicuous, and its thick walls and dark contents can be seen, *mei*. Surrounding this layer are two or three layers of small, thick-walled fibres. The outermost cells are radially somewhat elongated, palisade-like cells with definitely thickened walls (*mo.*, Plate 22, fig. 3, and text-fig. 11) which often have dark contents.

These cells appear to pass directly into the stone layer of the seed proper, and I see no reason to doubt that the middle fibres correspond to the middle fibre-layer of the seed, and the inner epidermis-like layer of the micropyle represents the last of the innermost layer of the seed-coat. In short, in the present instance, there is nothing to support the hypothesis that the micropyle is a peculiar outgrowth of a specialised inner integument, a point on which some (BERRIDGE, 1911; THODAY, 1911, etc.) have laid stress for the purposes of comparison with the Gnetales.

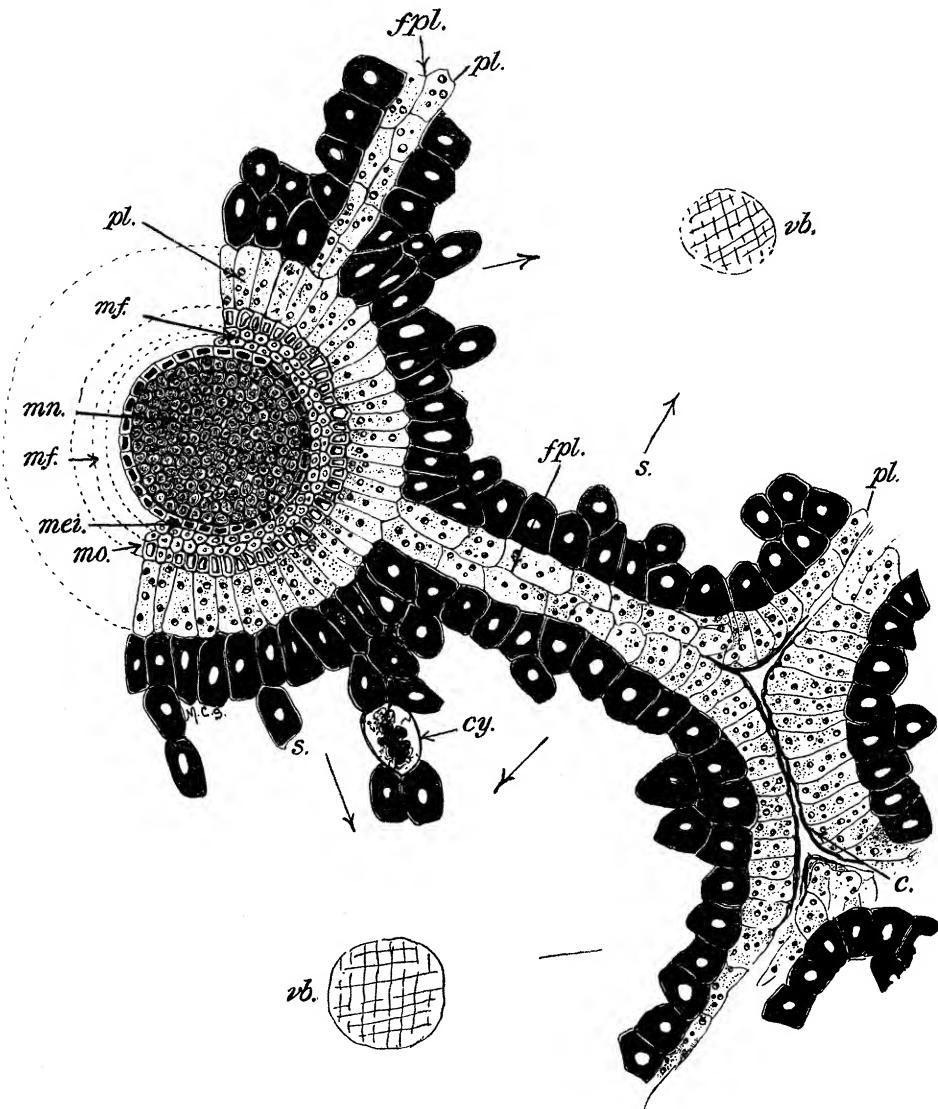
The greater part of the micropyle canal is circular, but at the top the cells of the innermost layer radially extend somewhat, and the opening becomes more like a slit between two lips; the fibres and the outermost layers remain circular in outline.

For the greater part of its length the micropyle is accurately plugged by a cylindrical outgrowth from the nucellus.

The Nucellus.—Save at the base of some of the seeds, the nucellar tissue is crushed back almost out of recognition and forms merely a thick, fibrous membrane during the greater part of the length of the seed. Towards the base, however, it can be seen well preserved in some instances. It is composed of closely packed cells, *n* in the photograph on Plate 19, fig. 7.

I have not been able to determine at what level the nucellus becomes free, a point of much interest in comparison with the older fossil, and other types of Gymnospermic seeds (see OLIVER, 1903, etc.). LIGNIER (1894) described *B. Morierei* as having its nucellus free only at the apex, but the photograph on Plate 19, fig. 7, is taken from quite near the base of the seed, and it and other seeds (see, e.g., Plate 21, fig. 11) suggest the possibility that the nucellus was free to the base in the present instance. I have not, however, been able to detect at any level a definite limiting layer to the ordinary nucellar tissues.

At the apex of the seed a solid mass of firm-walled cells completely fills the channel of the micropyle, as can be seen in photographs on Plate 20, figs. 20 and 3, and text-fig. 11, *mn.* It is cylindrical and has no flutings or complexities like the "lagenstome,"



TEXT-FIG. 11.—*B. albianus* sp. nov. Transverse section round micropyle and surrounding interseminal scales. *mn.*, nucellar mass plugging micropyle; *mei.*, inner limiting layer of micropylar tube; *mf.*, fibrous layer of micropyle; *mo.*, outer layer of micropyle; *pl.*, plastid-epidermal layer of scales, limiting them and adhering to micropyle; *c.*, cuticle of above layer; *fpl.*, similar layers fused, without cuticle; *s.*, stone cells of interseminal scales, among which are crystal-cells *cy.*; *vb.*, vascular strands of interseminal scales.

but fits tightly into the channel of the micropyle. It must be homologous to the "nucellar beak" (see OLIVER, 1900) though the cells here are apparently scarcely thickened, differing from the true "beak" cells in having relatively thin walls and much contents. The structure appears to be very similar to that described for

B. Morierei. Below this solid apex is an irregular space, which has every appearance of a pollen chamber, and which I incline to interpret as such. Transverse sections of this nucellar plug can be seen in which just one or two cells in the very centre of its solid mass of tissue are broken down (see Plate 21, fig. 18), others in which half of its diameter, accurately in the centre of the mass, is broken down, and others in which but a skin of the plug remains. This latter stage appears to join on to the crushed limit of the ordinary nucellus. This is all indicated in text-fig. 14, which is the diagrammatic representation of the longitudinal restoration of the seed.

The Endosperm.—The embryos are all somewhat contracted away from the membrane of the crushed nucellus in most cases, but there seems to be no recognisable trace of endosperm intervening. Of the few crushed cells preserved in possible positions in some of the seeds, it cannot be said that they clearly represent endosperm tissue. The seeds appear to be completely "exalbuminous."

The Embryos.—In the majority of seeds embryos are present. They have two cotyledons and are arranged, as in other described species of *Bennettites*, so that the radicle points upwards, and the two cotyledons lie in the seed-base. As the seeds are all cut transversely, only transverse or very slightly oblique sections of the embryos are obtained. The radicle, and also the regions of the plumule, all appear to be considerably contracted and crushed, and most of them are much retracted from the limits of the space in the seed which they may be supposed to have filled in life (see Plate 19, figs. 3, 4, and 5, in which a number of embryos can be seen within the seeds, and Plate 20, figs. 5, 6, 7, and 8). In several, the central vascular strands of these regions are visible (see, e.g. Plate 20, fig. 7), but these strands do not bear examination with the high power. In almost all of the embryos their tissues are permeated by innumerable fungal hyphae and strings of spores, which are here most conspicuous, but on the whole are absent from the rest of the tissues of seeds and scales, save in some places the "deliquescent layer" of the seed stalk sheath round the seed shows a similar fungal invasion.

In each cotyledon (a good example of which is to be seen in the photograph on Plate 22, fig. 5), a single row of vascular bundles runs. The number of strands in each cotyledon apparently varies a little; the two clearest examples showed respectively seven in each and nine in each, but it is very possible that, as is described by WIELAND (1911), the number was really an even one, and the fungal invasion of my seeds has concealed a small strand in each cotyledon. At first LIGNIER (1894) described seven bundles in each cotyledon of *B. Morierei*, but later (1904) he came to the conclusion that they were in pairs.

A series of photographs of various levels of embryos on the same scale of magnification is shown on Plate 20, figs. 5–9, in which the relative sizes of the parts can be seen. The two separate cotyledons, which lie in the lower half of the seed, are united at a level below the middle of the seed, so that the hypocotyl and radicle are relatively much more massive than is shown by SOLMS LAUBACH (1890–1) for

B. Gibsonianus or in WIELAND's species (1911, text-fig. 9). In my species, while the diameter of the seed is still almost at its greatest, the hypocotyl is seen as a central solid mass. In the upper region of the seed, where it is smaller and ribbed, the radicle is much contracted and corrugated.

Undersized and aborted seeds are very few in number in proportion to the large and embryo-containing seeds, but there are four or five of them. I have not observed an embryo in any of them, but the testa development is approximately normal. They do not appear to be of any interest, except that they are relatively so few in such a mass of fertile seed.

CONCLUSIONS.

In order to summarise and make clear the detail described in the preceding pages, I give three diagrammatic figures of the more essential parts. If these are studied, I think a fairly accurate view of the seed will be obtained, though I have been handicapped in making text-fig. 14, by the lack of any longitudinal, or even fairly oblique sections, of the seeds. In text-fig. 12 the series of diagrams of various critical levels of the seed shows the solid nature of the five apical ribs. In these diagrams, as in text-fig. 14, the complex layers of the integument proper are filled in solid black. The layer immediately outside this, which is an extension one of the seed stalk and tends to break down, and for which I have suggested the name "deliquescent layer," is omitted in text-fig. 12, but shown by small dots in text-fig. 14.

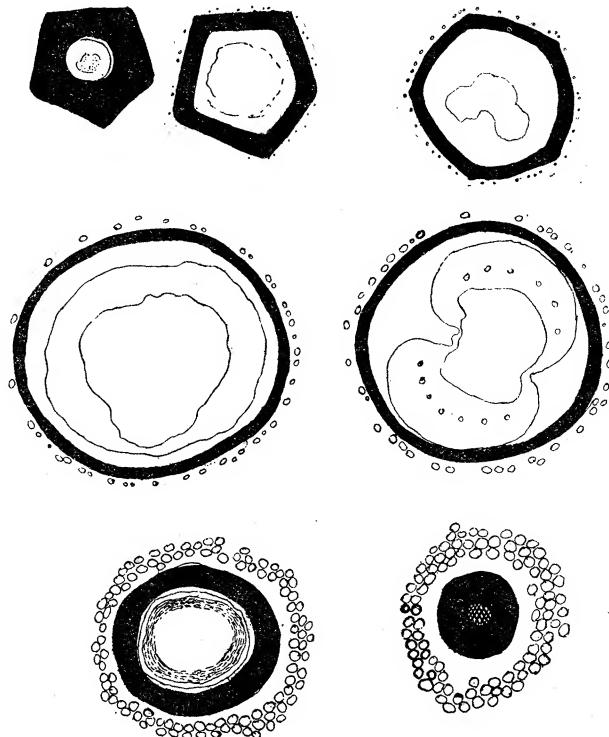
Perhaps the most striking feature of the seed covering, which is brought out clearly in the present account, is the "cupule" or "aril" of elongated tubular cells. If one visualises this intact, it would completely conceal the lower half of the seed, and so, in drawing an imaginary restoration of it, I have conceived of several of its outer cells as having been torn away, so as to reveal the seed in position within. This restoration is shown in text-fig. 13.

After having visualised this sheath in the present species, it becomes clear that *B. Morierei* must have been somewhat similarly enclosed, though LIGNIER's restoration of his seed (his Plate 20, fig. 28, which is oftener reproduced than his more accurate detailed drawings) does not appear to do justice to it. Comparisons of this queer "cupule" with the cupule of *Lagenostoma* (see OLIVER and SCOTT, 1904), which also surrounds a stony seed, and with the hair-like cells of the non-fused integument of *Physostoma* (OLIVER, 1909), are tempting, but such excursions into theory appear to me to be premature.

Unfortunately, in *Bennettites*, there are no vascular strands either in the integument proper or in the cupular coverings, so that, much less clearly than in the Palaeozoic seeds, do we know the equivalence of the parts.

This absence of vascular strands in the seeds, coupled with the very reduced state of the xylem in both seed-stalks and interseminal scales, suggests the possibility that

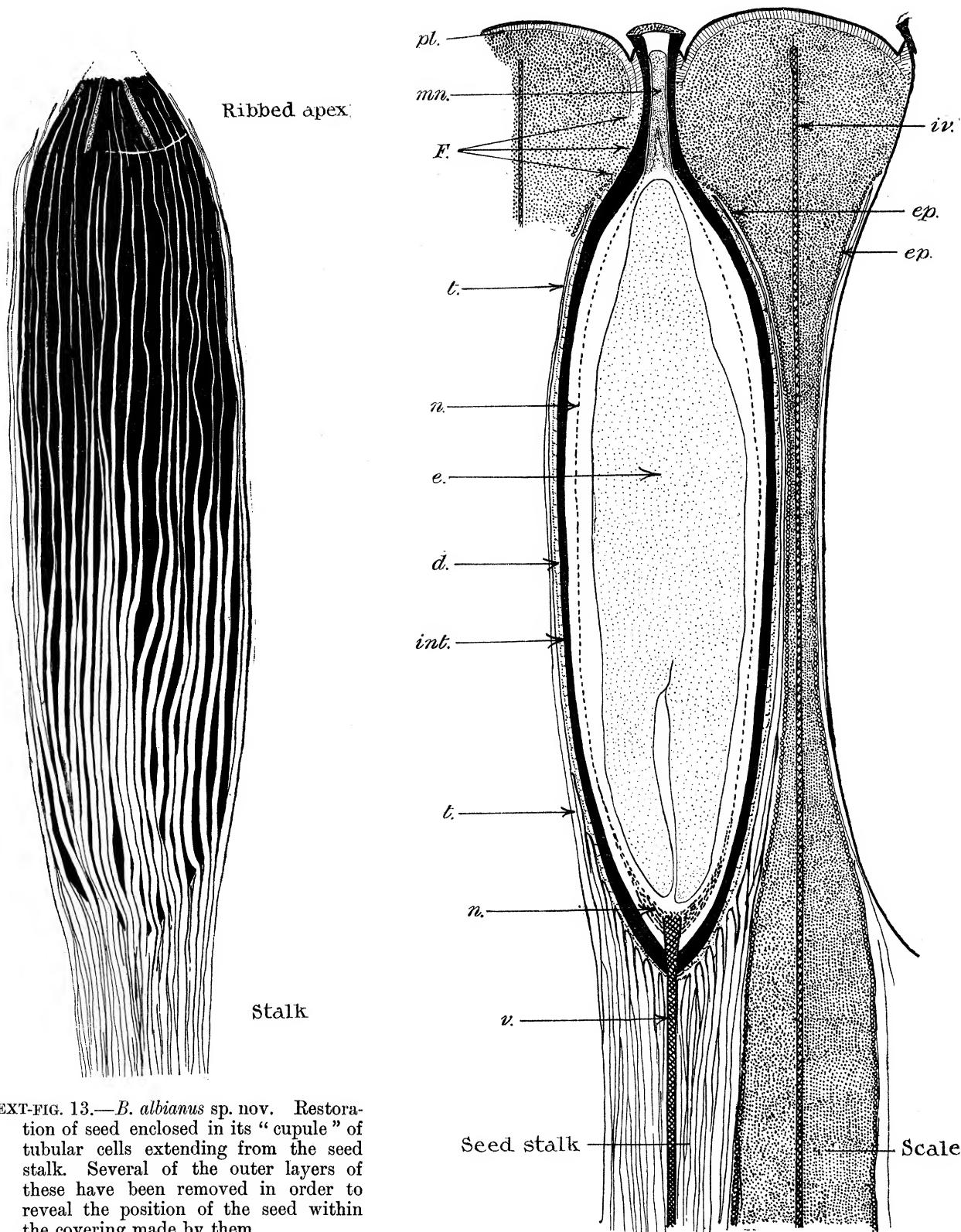
the peculiar hair-like tubular cells of the seed-stalk, which form the outer "cupule" also, may perhaps have exerted a capillary suction over water similar to that so conspicuous in the empty cells of the leaves of *Sphagnum*. In this way the growing ovules, and, later, the embryos, may have been kept in a suitable moist chamber. It must be remembered that, in the present species, the huge globose fruit had an outer shell of extreme hardness and induration, and that even the micropyles were accurately plugged up, so that if these tubular cells had had a supply of water, it would have kept the interior of the fruit adequately moist. The Cycadean stock is typically xerophytic, and their large cones are, in all species known to me, not only



TEXT-FIG. 12.—*B. albianus*. Series of diagrams of various levels of the seed. Compare with text-fig. 14.

protected externally, but well supplied by internal vascular strands (*cf.*, *e.g.*, STOPES, 1904), so that the apparent neglect of the water supply by the Bennettitean cones has appeared surprising. The possibility of special assistance rendered by the peculiar stalk-cells, which is suggested by the whole structure of the present species, would perhaps satisfy the requirements of the situation.

The longitudinal restoration of the seed and adjacent interseminal scales attempted in text-fig. 14, makes clear my interpretation of the relations of the parts. I do not know whether to describe the seed-coat as being one integument or five. In order to call it two, as is sometimes done, it is necessary arbitrarily to determine that certain layers are equivalent to an "integument," and certain others are not, but together go, two or three of them, to an "integument." LIGNIER clearly described the seeds



TEXT-FIG. 13.—*B. albianus* sp. nov. Restoration of seed enclosed in its "cupule" of tubular cells extending from the seed stalk. Several of the outer layers of these have been removed in order to reveal the position of the seed within the covering made by them.

TEXT-FIG. 14.—*B. albianus*. Diagram of restoration of seed and interseminal scales in median longitudinal section. The left side of the seed is imagined to have been cut at an angle of one of the five ribs, hence at the apex the stone is thicker on this side than on the other. Of the seed the parts are:—*int.*, seed coat, the layers of which are all represented by solid black; *n.*, nucellus; *mn.*, plug of nucellar tissue in micropyle; *e.*, embryo; *v.*, vascular strand of seed-stalk which dies out on entering nucellus; *d.*, "deliquescent layer," running up from seed stalk; *t.*, tubular cells of "cupule," running up from seed stalk; *F*, region of fusion of adjacent interseminal scales mutually, and to seed; *iv.*, vascular strand of interseminal scale; *ep.*, epidermis of interseminal scale; *pl.*, "outer plastid" layer of epidermis of scale, running also round micropyle neck.

as being "unitegumentées," but others who quote him (see, for instance, THODAY, 1911) speak as though he had described two integuments, and WIELAND (1911) talks about the "outer flesh" or "blow off," though this is one of the layers which LIGNIER showed were derived from the stalk.

There are clearly five layers of covering to the seed, viz.: (1) the inner thin-walled cells; (2) the fibrous layer; (3) the stone layer; these three form the seed-coat proper, and outside them come the two "cupule" layers, viz., (4) the "deliquescent" layer, and (5) the tubular cells of the "cupule." No single one of those has any more claim to rank as an "integument" than any other, and hence to be logical one has only three courses open to one: (a) to call all the layers, united, one integument; (b) to look on each layer as an integument and speak of five integuments; (c) to confine the integument to the inner three layers (which, by the deliquescence of the deliquescent layer, become separated from the rest, and form more strictly "the seed"), and call the outer layers "cupular." To speak of "two integuments," arbitrarily delimited, is merely to be subject to the hypnotic effect of preconceived ideas.*

This leads us to the comparisons with *Gnetum* in which the supposed double integument has played a considerable part in affording supposed likeness between the two seed-types. I agree with COULTER and CHAMBERLAIN (1910, p. 86) that "the present evidence for such connections is too slight to merit serious discussion." All the more so when the main point in the argument, viz., the supposed origin from the *inner* integument of the peculiar micropylar plug, is now shown to be mistaken.

As I have already stated (p. 408) the plug of tissue (which is clearly preserved in the present species) closing the micropyle appears to be an extension of the *nucellus*. In this I agree with LIGNIER's (1911) later and considered verdict against Miss BERRIDGE'S interpretation of this as an outgrowth from the "inner integument," and with him I can say that in my species also, "je conteste absolument la possibilité de cette interprétation du 'bec nucellaire' dont l'état massif est absolument *primaire* et qui, du reste, est totalement *indépendant du tube micropylaire*." (The italics are his.)

This tissue, as I indicate in text-fig. 14, is nucellar. Whether or not the space which lies in its lower portion is the true pollen chamber, or part of it, is not easy to determine with certainty; but experience of the pollen chambers of Cycads leads me to suspect it of being so. Its appearance is in favour of the view. The plugging of the micropyles led LIGNIER (1911) to the conclusion that his species *B. Morierei*

* Since completing this paper I have received Prof. PEARSON'S new work on the morphology of *Gnetum*, in which he figures four distinct envelopes to the seed, each with its vascular system. This conclusively supports the view expressed below that the previously published detailed comparisons between *Gnetum* and *Bennettites* were premature (see PEARSON, 'Trans. Linn. Soc.', vol. 8, Part 8, 2nd series, Bot., Pl. 31, fig. 2).

must have been parthenogenetic, but I do not see the necessity for the conclusion. I think it much more probable that at the time of *pollination* (which may have been much antecedent to fertilisation) the sizes and relationships of the parts of the ovulate cone were very different from what they are in the mature fossils we have preserved. Experience of the pollination of *Ginkgo* (which is so often incorrectly described as being similar to that of Cycads) shows that the extremely young, almost unenclosed nucellus may receive the pollen grains; and almost all the specific parts of the seeds grow up later. It is, I think, extremely probable that in the new *Bennettites*, and also in *B. Morierei*, the very young micropyles were not plugged at all, but gaped widely, and the pollen was received on the nucellus, the apex of which retained its meristematic state and thus grew to overtop the region of the actual pollen chamber, and ultimately plugged the micropyle as the fruit increased in size and hardened. I incline therefore to discard the view that the Gault forms necessarily approached extinction through or *pari passu* with a parthenogenetic habit.

Another problem raised by the genus as a whole, but more vividly presented by the new species, is the question of seed dispersal. The complete fusion of the stony scales, which has been described in this new species, must have meant that the fruit as a whole had a hard, uniform shell of great stability and strength; externally it was bossed by the pattern of the terminations of the separate interseminal scales composing it, and internally it frayed out to the stalks of the scales, but the solid, coconut-like shell firmly enclosed the ripe seeds. The seeds did not rattle about in it loose, for their ribbed apices also were wedged into the solid mass. It is not impossible that the hard fruit had considerable drouth to withstand (the group of the Cycadales is a typically xerophytic one), and if so, and if my interpretation of the curious tubular cells of the stalk (see p. 401) is correct, then this hard shell enclosed a moist mass which could indefinitely withstand arid conditions. Presumably the shell ultimately rotted or broke apart, or was a plaything for some animal which eventually smashed it. The embryonic radicles are oriented in such a way as to anticipate a normal growth of the embryo through the seed-micropyle.

The giant size of the present species raises a point of general interest in connection with the profound, almost philosophical results obtained by animal palaeontologists. In many families of animals, giant forms appear shortly before the extinction of the group. The new *Bennettites*, which is the giant fruit of the family, and occurs in the highest horizon in which the group is known, may be considered to be a corresponding phenomenon. But this tempting conclusion must not be accepted too readily. In the first place, this is a giant *fruit*, and in so many of the modern Cycadales giant fruits are borne on small or almost pigmy vegetative plants. The giantism of the animals approaching extinction was not in their reproductive organs, but in their general bodies. The comparison with the animals, therefore, is obviously an insecure one. We are, alas, too little acquainted with the profound laws of

palæobotanical evolution to know the significance of the isolated phenomena we observe. Only the collection of innumerable more data will remedy this.

The above species is called *Bennettites albianus*, sp. nov., from the horizon (the Gault or Albian) in which it was found.

Diagnosis.

Fruit : Ovulate cone, not less than 70 mm. in diameter and probably much more.

Seeds : Innumerable, 600 or more in a single transverse section ; five-ribbed, much elongated, torpedo shaped, 5–6 mm. long, and about 1·2 mm. in greatest diameter. Seed with many-layered integument, enclosed in cupule-like extension of tubular cells of the stalk. Micropyles blocked by plug of nucellar tissue. Interseminal scales completely mutually fused round apex of seed and with seed tissues.

Embryo : With two cotyledons ; radicle and hypocotyl relatively massive.

Scales : Externally covered by well marked “plastid-layer” which runs round collar of micropyle.

Horizon : Gault (Albian).

Locality : The Warren, Folkestone, Kent, England.

Type : Entirely cut up into sections, shared between Mr. G. WALTON, F.L.S., Chairman of the Folkestone Museum ; the Geological Dept., British Museum (Nat. Hist.) ; and (one slide) the Stopes Collection, University College, London.

BENNETTITES MAXIMUS, CARRUTHERS.

Plates 23 and 24, Text-figs. 15–25.

Since CARRUTHERS diagnosed, but did not describe, this plant in 1870, only three passing references to it had been made in the literature of palæobotany, until its external features, and what could be made out of its anatomy with a hand lens, was described in the British Museum Catalogue of the Lower Greensand Flora (STOPES, 1915).

The unique specimen evidently merited more attention than this, for though the British Lower Greensand form *B. Gibsonianus* is the type of the important family of Bennettitales, yet we know all too little of the British varieties of the family, owing to the extreme rarity in this country of specimens anatomically preserved.

The polished surface of *B. maximus* promised so well that, at my request, the Director of the Geological Survey most kindly arranged for a series of microscopical sections to be cut in various directions so that the details of the specimen could be studied. Upon these sections the following description of the species is based. I wish here to acknowledge gratefully the kindness not only of the Director, but also of the Palæontologists of the Geological Survey, who took much trouble to ensure that the specimen was cut in the most favourable directions. Mr. JOSEPH LOMAX did the cutting, and some magnificent sections resulted. Not only are various

features of the anatomy of this plant beautifully preserved, and justifying CARRUTHERS' identification as an independent species, but the species reveals itself as being particularly interesting in having *young cones*. These are the first bisporangiate cones in anatomically petrified material for this country, and are, moreover, preserved at a younger stage of their development than those of any described species of *Bennettites*.

GENERAL DESCRIPTION.

This trunk is somewhat larger than that of *B. Gibsonianus*, its contemporary, while its vascular cylinder is notably more slender, and its cones much younger than in the type species of the genus. Its external features are not well preserved, owing to the pounding and abrasion it had suffered on the sea-shore, but its somewhat flattened, oval contour is apparent. This appears to have been natural and not a result of crushing, so far as can be judged from the undistorted state of the internal tissues.

CARRUTHERS (1870, p. 699) noted the "very slender woody cylinder," which is a conspicuous feature of this trunk. This can be well seen in fig. 1, Plate 23, but to realise its true proportion it must be remembered that at *p* there would be an unbroken extension of pith for 21 cm. were it to be filled in on the same scale of magnification as the enlarged segment photographed, the actual diameter of the pith being $14\cdot5 \times 7$ cm. Fig. 2, Plate 23, illustrates very well the radial view of the wood cylinder, and shows the slight increase in the amount of the wood lower down in the trunk, and also the sprayed out branching of the strands passing into the leaf-bases.

Partly owing to the surface weathering, and partly to the fact that the young, undeveloped cones are deeply embedded in the leaf-bases, the fructifications cannot, unequivocably, be recognised in the external surface of the specimen.

The dark, hard texture of the petrifying medium in which the tissues are well preserved appears, so far as can be judged without analyses, to be preponderatingly composed of silicates with a small admixture of carbonates.

DETAILED DESCRIPTION OF VEGETATIVE ORGANS.

The Trunk.

The massive *pith*, which is $14\cdot5 \times 7$ cm. in diameter, appears to consist solely of ground-tissue, without any admixture of accessory or centripetal vascular strands. Its cells are, on the whole, poorly petrified. In the uncut polished surface certain white flecks suggest the presence of resin or gum canals, but I have not been able to identify any in the actual sections. In the sections scattered throughout the pith, numerous large cells can be seen which have thick brown walls, with numerous pits and definite pitted areas in them. These cells seem to be identical with the similar ones in the leaf-bases, and as they are there better preserved, reference should be made to p. 422 and text-figs. 20 and 21. These cells in the pith are roughly spherical

or ovoid, measuring 80μ or more in diameter, and they are scattered thickly; but though in most places they are the only cells preserved, they appear to have formed but a part of the tissue, and to have been surrounded by smaller thinner walled cells which have generally disappeared. They are best seen in the lower half of section No. 28290.

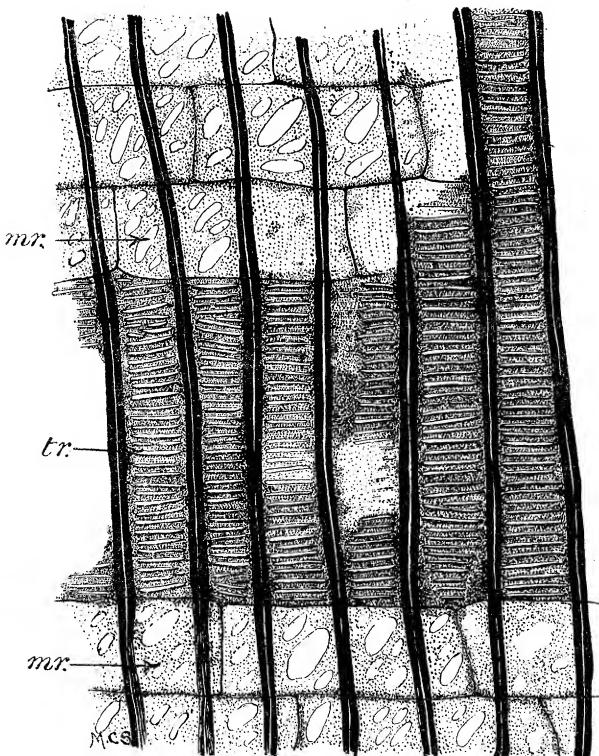
The *vascular cylinder* forms a slender, hollow monostele immediately surrounding the pith and averaging $14\cdot5-15\cdot5 \times 7-8$ cm. in diameter. The secondary xylem and phloem originate from a single cambium. As can be well seen in fig. 2, Plate 23, there is an increase in the thickness of the slender vascular cylinder towards the base of the trunk, the total thickness being 6 mm. about the middle of the trunk, and 9 mm. 11 cm. lower down.

The relative proportion of xylem to phloem is the reverse of that usual in the vascular cylinders of the higher plants, for the xylem measures on an average in radial thickness only about one-half of the phloem. This can be seen in the upper part of fig. 2, Plate 23, where the longitudinal white streak separates the xylem on the right from the phloem on the left. In the middle of the trunk there are 2 mm. of xylem to 4 mm. of phloem and lower down 6 or 7 mm. phloem to about 3 or 4 mm. of xylem. At the outgoing of the leaf-traces the xylem locally thickens.

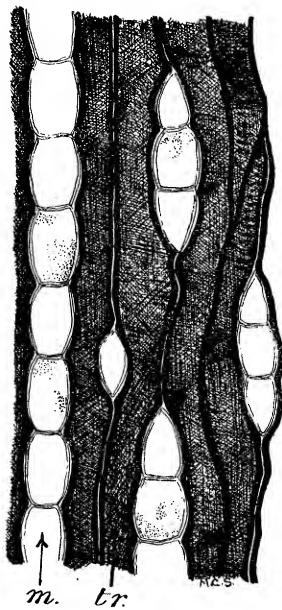
The *xylem* is apparently all centrifugal, see Plate 24, fig. 7, the first formed elements are small, averaging $12-20 \mu$ in diameter, with excessively thick black walls. In longitudinal section I have not been able to detect any spirally thickened xylem; those nearest the pith, which show the pattern of their walls, have slits similar to the scalariform thickening of the bulk of the tracheids, but slightly more irregular.

The *secondary xylem elements* average $40-50 \mu$ in diameter. They are arranged in radial series, mostly in single rows, sometimes in two or three adjacent rows, separated by medullary rays. The individual tracheids are squarish in outline in transverse section, with thick black walls. In longitudinal radial section the characteristic scalariform pitting of all these elements can be well seen (see text-fig. 15, *tr.*). In tangential section the tracheids curve round the large medullary ray cells, and have bulgy irregular outlines so as to fit into the available spaces, see text-fig. 16, *tr.* I have detected no pitting in the tangential walls in the majority of elements, though very short scalariform pits are present in some.

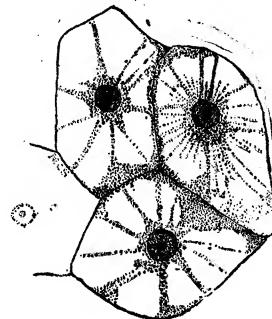
The *medullary rays* are almost entirely uniseriate, though in a few places the centre of the ray is biserrate. (The rays of most of the Cycadales are bi- or multi-seriate.) The rays are conspicuous, the elements composing them being large cells, in the main rectangular, though they vary greatly in size and outline. Some, if not the majority, of the cells show obliquely placed, rather irregular slits in their radial walls where they cross the tracheids. So far as I am aware such pitting of the radial walls of the medullary rays has not been noted in any species of *Bennettites*. Though in some instances these slits may be due to the breakdown of the walls, yet the perforation is so noticeable a feature in large areas that it seems to be natural.



TEXT-FIG. 15.—*B. maximus*. Longitudinal radial section of wood and medullary rays. *tr*, tracheids with scalariform pitting; *mr*, medullary rays with pits in the tracheid-areas of the medullary rays.



TEXT-FIG. 16.



TEXT-FIG. 17.

TEXT-FIG. 16.—*B. maximus*. Tangential longitudinal section of the wood. *tr*, tracheids; *m*, medullary rays.

TEXT-FIG. 17.—*B. maximus*. Cells of the ground-tissue showing structures strongly resembling nuclei suspended by strands of protoplasm. [Slide 28.]

Certainly, in several places, the pitted areas in the medullary ray cells have every appearance of being original and not petrifact. The character of the medullary ray cells can be seen in radial section in text-fig. 15, *mr.*, where the pittings in the radial walls are shown in relation to the tracheids.

In tangential section the shape and size of the ray cells is shown in text-fig. 16. I have not observed unimpeachable pitted areas in the end walls of the ray cells; but though one would not anticipate them in this position in this family of plants, I nevertheless suspect them of being there, from the presence of certain rather obliquely placed walls seen in transverse sections which appeared to be distinctly pitted. These pitted areas have simple flat pits, and are not like the end-wall pitting in the Abietinean ray.

The position of the *cambium* was evidently quite normal, and was continued through the outgoing leaf-traces. It is clearly indicated by a break in the tissues, where a narrow zone, evidently of soft cells, is poorly preserved.

The massive *phloem* is composed of thick-walled fibres which alternate singly in radial sequence with thin-walled elements. This can be seen in the portion of the phloem shown in Plate 24, fig. 7. The fibres average about 25–40 μ in diameter, and run approximately straight for long distances. The appearance of the phloem in detail is quite similar to that of the other described species of *Bennettites*, though it is present in a larger relative quantity than usual. Text-fig. 41, E, page 76, or WIELAND's (1906) description of the American *C. Wielandi* might have been drawn from the present specimen, so like is this feature in the various species of *Bennettites*.

The *cortex* is quite similar to the pith, and appears to show no distinctive feature. It is rather poorly preserved, but in a number of places the peculiar pitted cells as described in the pith and leaf-base tissues can be seen. I have not observed any resin cells or gum-canals.

The nucleus-like bodies mentioned by WIELAND (1906) as being conspicuous in the medulla cells of his species, are paralleled by roundish bodies in a great many of the cells of the cortex in the present species, which are sometimes remarkably like nuclei (see text-fig. 17, where even the suspending threads of protoplasm can be seen). In spite of their extraordinarily nuclear appearance, however, the fact that in some places there are more of them than there could have been nuclei, and that in some regions where the tissues have broken down and mineral matter only is present, identical bodies are to be seen, some of which are rather larger than the nucleus-like ones, makes me hesitate to accept the obvious conclusion that these bodies are true nuclei. It may well be that nuclei formed the centres for the accretion of certain mineral substances which also collected round other centres in different parts of the plant in process of petrification.

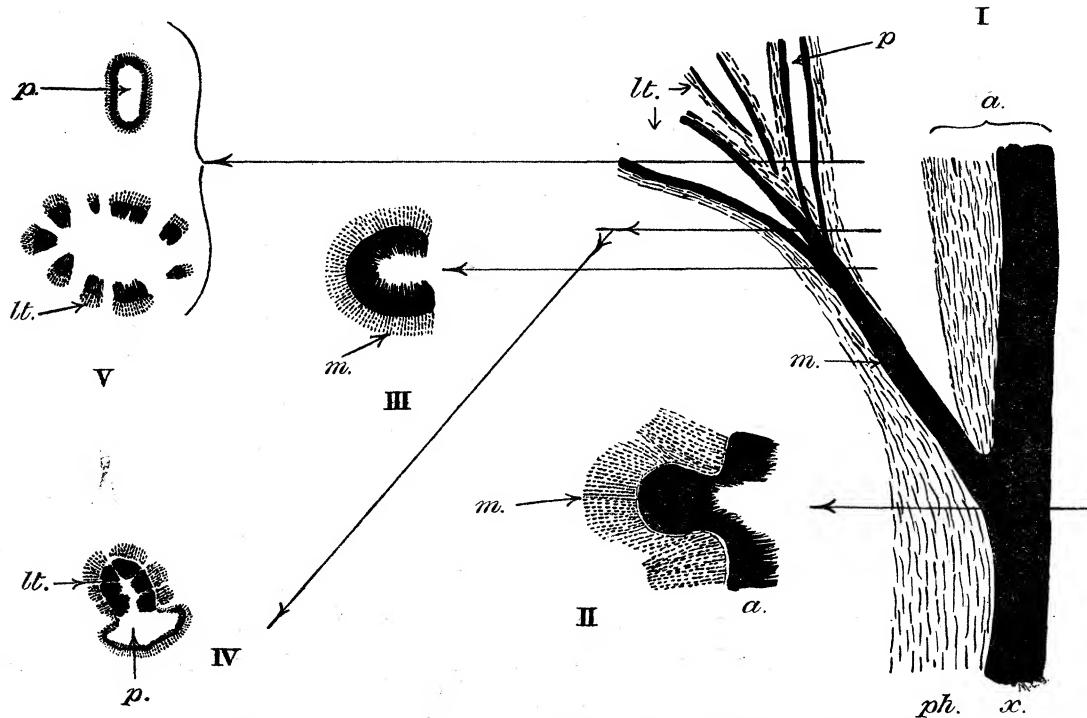
The *meristyles*, which run in the cortex, leave the main cylinder as stout loops, and break away from the axis as thick crescents of secondary wood and phloem. In the course of the passage of each out through the ground-tissues of the main trunk, the

curve of the arc rapidly increases, and when at about 2 cm. from the main cylinder, in horizontal distance, the xylem and phloem strands curve and twist and break up into two systems of strands, viz., the peduncle cylinder, which is a closed ring, and the leaf-base strands which form an irregular ring or horse-shoe of unequal collateral bundles.

In longitudinal section this curving and spraying out of the meristele as it passes towards the leaf-base is well seen at *s* in Plate 23, fig. 2, which is a photo of a splendid radial section of the trunk.

The meristoles take a direct course outwards to their respective lateral organs, a feature which, as earlier writers have pointed out, is common to the Bennettitales.

Though the number of sections in series is not sufficient to determine absolutely the minute details of their course, it appears that, in the present species, each single large meristole leaving the main cylinder moves upwards at an angle of about 30° , and, when the strand is about 2 cm. in a horizontal direction and about 3 cm. in a vertical direction from the main stele, it breaks up almost simultaneously into two or three large leaf-trace strands (which further rapidly subdivide), and into a small circular cylinder, which goes off to one side, and soon enlarges, becoming the peduncle central cylinder. The course resembles a sudden spraying out of a jet, and is roughly indicated by the diagram in text-fig. 18, I, which represents what happens in the cortex of the main trunk.



TEXT-FIG. 18.—*B. maximus*. Diagram of the exit and branching of meristole from main axis. *a.*, vascular tissue of axis; *m.*, vascular tissue of meristole; *x.*, xylem; *ph.*, phloem; *lt.*, leaf-traces; *p.*, ring of peduncle cylinder. I, radial longitudinal section; II, III, IV, and V, transverse sections at levels of the corresponding arrows.

I have not a sufficient number of slides to establish with certainty that this course is always followed by the bundles of the present species, but, so far as the indications of the material available go, *B. maximus* seems to have a simpler method of providing for its peduncle cylinder than that described by WIELAND for *C. Wielandi*, for instance. The figure of previously described members of the group most nearly comparable with it is fig. 1, Plate 2, of CAPELLINI and SOLMS' (1892) description of *C. Pirazzoliana*, but the latter differs essentially in showing the anastomosis of the leaf-trace bundles. Moreover, in the drawing, the strands are made to appear as though they took their rise in the phloem region, while the crossing out of the strands through the phloem is well shown in the photograph of *B. maximus*.

The peduncle strand, once in the lateral axis of the cone, itself gives off series of horseshoe-shaped strands to its own surrounding bracts, while, in the leaf-bases, the leaf-trace strands further subdivide.

I have observed no centripetal xylem in the strands while they are in the cortex of the main trunk, or elsewhere.

THE LEAF-BASES.

As has already been mentioned, no accurate observations of the size, shape, or arrangement of the leaf-bases had been made on the exterior of the specimen, owing to the weathering it had suffered.

The leaf-base is best seen in the tangential sections of the trunk, which were cut to show the cones. Here, on a level with the base of the peduncle of the cone, and consequently comparatively close in to the main axis, the leaf-base measures about 2.5×1 cm.

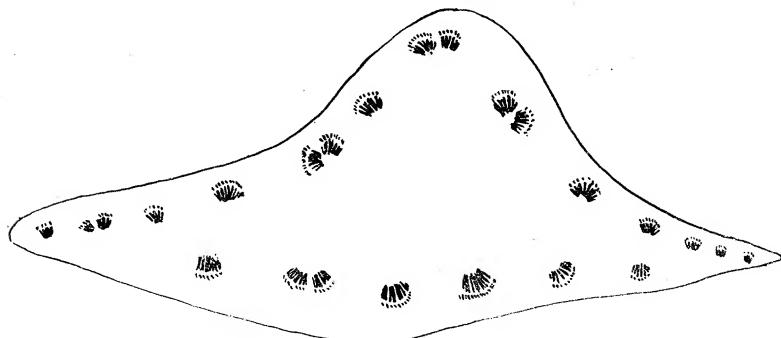
The outline is roughly rhomboidal. A number of small vascular bundles run rather near to the margin, and are oriented in two series, lying face to face (see text-fig. 19).

Though pieces are broken out of the leaf-bases, locally the tissues are beautifully preserved.

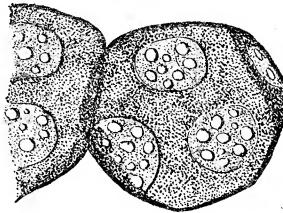
The *epidermis* is generally badly preserved, but in a few places it can be seen to have been protected by a fairly thick cuticle.

The *ground-tissue* essentially resembles that of the pith and cortex, but the cells are rather smaller and more closely packed, and there is a greater proportion of the thick-walled pitted cells, like those mentioned in describing the pith and the cortex. In the leaf-bases these remarkable cells culminate in numbers and differentiation. The entire ground-tissue appears to consist of soft-walled tissue, very thickly sprinkled with these thick-walled, pitted cells, which amount to half or more of the tissue of the whole leaf-base. I have seen no evidence whatever of resin or gum canals, which are always described as being present in *Bennettites*, and the impression created by the well-preserved leaf-bases is that they were originally absent here,

and that this species did not possess them. In transverse section some of the curious thick-walled cells simulate them to some extent. And it is not impossible that these very peculiar cells may have contained a watery type of "gum," and thus fulfilled the function of gum canals, a function which, owing to the prevalence of gum canals in all the living Cycads and fossil Bennettitales, appears to be inherently necessary in the physiological economy of the family.



TEXT-FIG. 19.



TEXT-FIG. 20.

TEXT-FIG. 19.—*B. maximus*. Outline of leaf-base showing the orientation of the vascular bundles. $\times 4$.

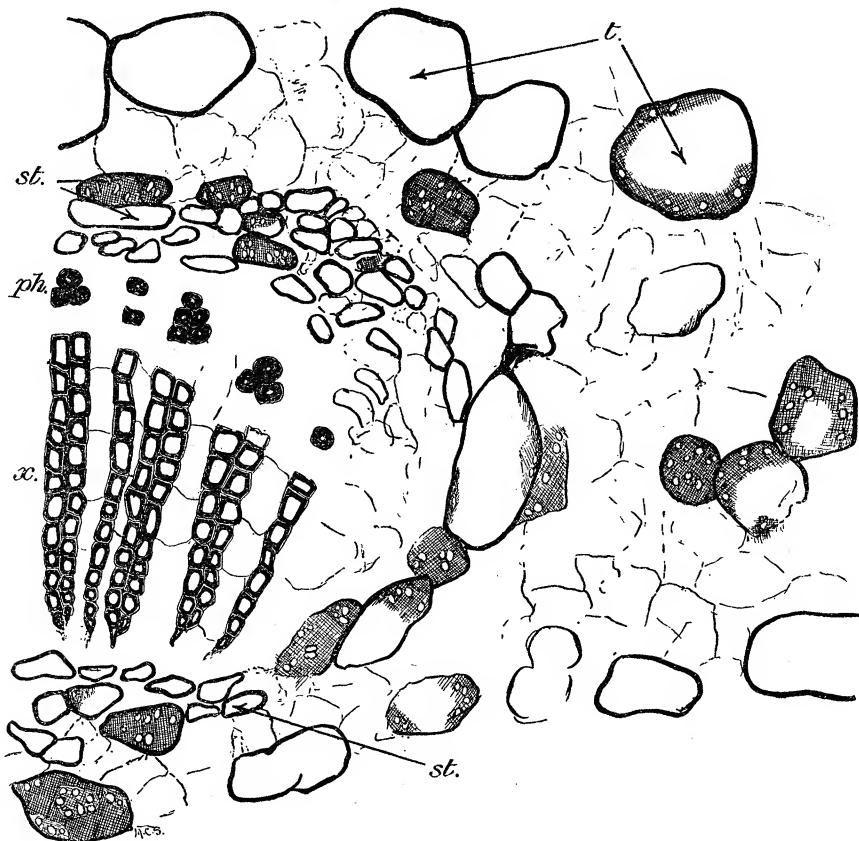
TEXT-FIG. 20.—*B. maximus*. "Transfusion cells" of ground tissue of the leaf-base, with pits in pitted areas.

I call these cells, provisionally, "transfusion cells." Though these remarkable cells have several features quite unlike any known transfusion-tissue, for the present the name may serve for them, as they have certain characteristics of true transfusion-tissue. They are noticeable, globular cells, roughly spherical, or oval, averaging about $80\ \mu$ to $120\ \mu$ in diameter. Sometimes they lie isolated among the soft tissue of the leaf-base, but they are so numerous that they are nearly all in contact with at least one similar neighbour, and, in many cases, whole patches of them lie together.

Their walls are thick and brown, and are very distinctly pitted. In some the pits lie in definite oval or circular pitted areas. Such cells are shown in text-fig. 20, and can be seen quite clearly in the photographs (Plate 23, figs. 3 and 4). In others one wall may have the pits in definite pitted areas, and the other walls have isolated pits; in still others isolated pits perforate all the walls. These cells are crowded throughout the leaf-base; almost touching the epidermis, scattered right through the centre of the tissue, and often crowded near the vascular bundles. It is to be noted that though they are often thickly clustered round the bundles they are almost as numerous elsewhere.

Round each vascular strand there is something in the nature of a rather small-celled bundle sheath, more or less definitely delineated (see fig. 3, Plate 23, text-fig. 21). It is to be observed that these curious large "transfusion cells" merge with this sheath, which is formed from smaller individuals of the same type of cell. This may be seen in many of the sections, but best in Slide 28305. The arrangement of

the cells of the ground-tissue and bundle-sheath is shown clearly in text-fig. 21, where it may be seen that the loose, rather irregular sheath is composed of pitted cells, *st.*, quite like the larger similarly pitted cells *t* which lie all through the ground-tissue. This is still more clearly to be seen in slightly oblique sections, where practically every one of the sheath elements show the nature of their pitted walls. The bundle sheath of the leaf-base bundles, therefore, is merely composed of smaller individuals of the characteristic "transfusion-tissue" which is distributed all through the leaf-base. When it is remembered that these same curious "transfusion-tissue" cells lie not only in the leaf-bases, but also in the cortex and in the pith of the main trunk, as well as the peduncle and bracts of the cone, the quite exceptional nature of this arrangement will be realised.



TEXT-FIG. 21.—*B. maximus*. Transverse section of part of leaf-base bundle and surrounding ground-tissue. *x.*, xylem; *ph.*, phloem; *st.*, "transfusion elements" of bundle-sheath; *t*, larger "transfusion" elements of the ground tissue. [Slide No. 28.] Note.—Not all the cells are filled into the drawing.

A word must be said about the relation of these cells to the other tissues.

The presence of transfusion-tissue in the mesophyll of Cycads and other gymnosperms has long been known, and was particularly studied by WORSDELL (1897). The relation between the centripetal xylem and the lateral transfusion-tissue of the vascular bundles is now generally accepted. When dealing with the leaves of *Cordaites* I

noted that the definite bundle-sheath seemed to be a compound of double origin, the inner transfusion-tissue of *vascular* origin (from the centripetal xylem), the outer of mesophyll origin. With the current interpretation of the Bennettitalean leaf-base bundle, as being mesarch, it is arguable that the sheath cells on the xylem side might very well be interpreted as centripetal xylem elements, particularly were they seen only in transverse section. They are, however, traceable as being continuous with the larger "transfusion cells" scattered all through the plant, and I find it impossible to draw any distinction between them. In no case in the vegetable kingdom, so far as I am aware, do extensions of the centripetal xylem, dissociated entirely from their proper place, spread not only throughout the leaf-bases, but all through the cortex and the massive pith of the main trunk—we must remember in this plant that the pith is huge, measuring 14×7 cm. in diameter, and all through it these cells are scattered, though not quite so thickly as in the leaf-bases. Possibly the smaller cells of the sheath may best be held to be modified elements of centripetal xylem, and the large transfusion elements to be specialised mesophyll tissue, which have taken on identical characters. The distribution of these cells distinguishes this species from all other forms described hitherto in the *Bennettiteae*.

The *vascular bundles* are simple collateral strands, of which the general distribution has been indicated (see text-fig. 20). The details of the xylem and phloem arrangement are perfectly simple, the whole of the xylem evidently being centrifugal (see text-fig. 21, x) unless the queer "transfusion cells" of the sheath be interpreted as modified centripetal xylem. I have carefully examined every bundle in the leaf-bases, and in none do I find an element which can be truly described as ordinary centripetal xylem. This is noteworthy because the leaf-base bundles of *Bennettites* are generally described (see SEWARD, 1897; WIELAND, 1906; SCOTT, 1909, and others) as being entirely like the leaf-bundles of Cycads in their mesarch structure. LIGNIER (1901), however, described the bundles of *C. micromyela* as being universally without centripetal wood, and in this particular the two species are alike; LIGNIER's species, however, has large and conspicuous gum canals, and is not like *B. maximus* in general.

Ramenta.—The characteristic Bennettitalean multicellular ramenta have been so fully described for other species and so well figured by WIELAND (1906) that there is no need to particularise them in the present species. They are, however, rather exceptionally numerous, as can be judged by the large areas occupied by masses of them in the transverse section of the main trunk, where they occupy a greater area than the leaf-bases they surround (see Plate 23, fig. 1).

This is perhaps correlated with the fact that the cones are exceedingly young, and the plant was thus petrified in this undeveloped state, viz., at a time when the protective scales must have been at the height of their usefulness, and consequently proportionately bulky.

THE CONES.

In the small part of the trunk drilled out to be cut in series for the fructifications, two cones are present, which, for convenience of description I shall call cone X and cone Y. Photographs of these two cones, and the leaf-bases among which they lie, can be seen in figs. 1, 2 and 3, Plate 24. Their extremely small size will be realised when it is noted that these photographs are magnified by approximately one and a half diameters. Cone X shows best the fertile tissues, which appear as dark circles on the upper side of figs. 2 and 3; cone Y shows best the tissues of the pedicel. Cone X at the region of its scale tips has a total diameter of less than 1·5 cm., while the fertile, central portion of the cone measures only 6 mm. in diameter, contrasting with the 20 mm. or more of the corresponding region in the riper cones of *B. Gibsonianus*. Though also actually small, the pedicel is proportionately much larger in these young cones, and in cone Y measures 1 cm. in diameter. The distance apart of the two cones is worth noting, for it also is small. From centre to centre cone X and cone Y measure only 2·5 cm. apart, leaving consequently a region of 1 cm. between the two cones. It appears that the cones must have been very thickly scattered over the surface of the main axis if this is a representative portion of the trunk, as there is no reason to doubt. Owing to the very heavy expense of the section cutting, further areas were not cut.

The tissues of the fertile portion of the cone, which looks so black in the sections (see figs. 2 and 3, Plate 24), appear to owe this dark coloration less to imperfect preservation than to the dense nature of the young tissues, whose closely packed cells are filled with finely granular dark deposit. That these nascent tissues are well preserved is indicated in the enlarged photos (figs. 5 and 6, Plate 24), though the combination of rather delicate walls and packed, dark granular contents blurs the photographic representation.

To the eye, under the microscope, the tissues have the appearance one would expect from actively growing dense masses of meristematic tissues.

In essentials (*i.e.* in the arrangement of a series of bract scales in close succession round the pedicel, succeeded by the fertile portions with the cone terminating the pedicel), this species resembles the type of the Bennettitalean fructification as revealed by WIELAND's work; but, owing to the extreme youth of the fructifications, the characters and proportions of the parts differ essentially from those of any other member of the family described hitherto.

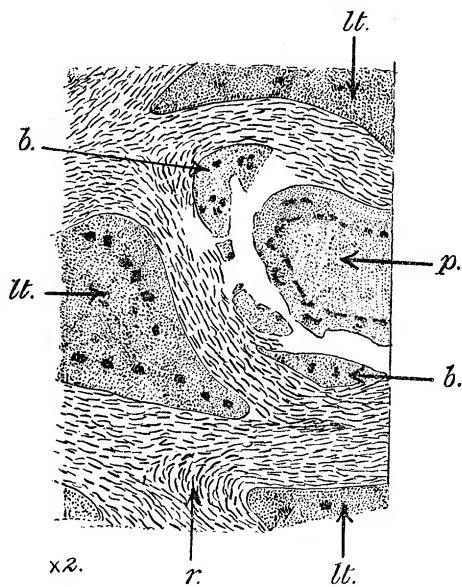
The scales surrounding and overtopping the fertile portions can be seen in transverse section cut across towards their tips in photo. 1, Plate 24, at X. Sections from lower in the cones show larger scales, and their more massive bases can be well seen in sections cut from levels low in the pedicel. The actively growing fertile part of the cone, seated terminally on the pedicel, is very small and restricted, and in cone X appears only in three sections. Allowing an average of 2 mm. between each

section, which is that estimated as a fair average in work of this type, this gives a probably vertical height of the whole cone of about 5 mm. In this space the rudiments of both the ♂ and the ♀ organs are recognisable. The fact that there are distinct indications of male organs is most interesting, as hitherto we have had no petrifications of bisporangiate *Bennettites* from this country or of this geological horizon, though older "impressions" of Williamsonias are comparatively common, and THOMAS (1915) has recently obtained many specimens of an interesting new form of bisporangiate axis in an allied genus.

The diagram in text-fig. 25, p. 432, shows a restoration of the relations of the parts of *B. maximus* which is based on the series of transverse sections of the two cones available. There are no vertical sections of cones with which to compare it, so the figure is avowedly crudely diagrammatic, but as it brings out the marked differences in the proportions of the parts between this species and WIELAND's bisporangiate cones, it may be of interest to compare it with his diagrams.

The details of the various parts of the fructifications will now be considered.

The Bract Scales.—As in all other *Bennettites* these are surrounded by thickly packed ramenta, of which no description is needed. The scales are massive where they leave the peduncle, as can be seen in many of the sections, and is shown in text-fig. 22, where *b*, *b*, are bracts which have quite recently separated from the cone



TEXT-FIG. 22.—*B. maximus*. Outline sketch of the base of cone Y and the surrounding leaf bases and ramenta. *lt.*, leaf-bases; *r.*, ramenta; *b.*, bracts of cone; *p.*, peduncle of cone with vascular cylinder and horse-shoe shaped meristoles. [Slide 28305.]

peduncle, *p.* In the present species, the peduncle gives off a small curved meristole to each bract, which is rapidly divided to form a larger number of vascular strands in the free bract.

Before the bract scale has entirely detached itself from the pedicel there are in it

three or more strands, placed at varying angles, which are speedily subdivided into seven bundles at least. In their lower regions these scales are exceedingly like the leaf-bases in their structure, and there seems no actual difference between the ground tissue of the two organs, save that the bract scales are a little less solid and their cells a trifle smaller than in the more massive leaf-bases ; as also the vascular strands, though entirely similar in organisation, are smaller and contain fewer elements. The curious transfusion-tissue cells, already noted in so many parts of this specimen, are to be seen in numbers in the scales, and differ not at all from those in the leaf-bases, save that their largest cells do not reach quite so great a size as the largest in the leaf-bases. On the average they are identical.

I can detect no convincing gum canals, and am inclined to believe that they were absent here too, but there are a few broken spaces which might perhaps bear the interpretation that they represent gum passages. The bracts show none of the barred cells which form such a characteristic ground tissue in *B. Gibsonianus* and other species of the genus, and are illustrated by CARRUTHERS (1870), WIELAND (1906), and others. The bases of the scales are better preserved than the middle and upper regions, where, though they are clearly recognisable as in fig. 1, Plate 23, c, and fig. 1, Plate 24, the tissues are contracted and poorly petrified.

The *peduncle* of the cones is relatively massive and important. That of cone Y can be seen in text-fig. 22 at p. The peduncle averages about 1 cm. in diameter and is very roughly circular, its outline, being dependent on the numerous outgoing scales, is variable. In the best preserved sections (e.g., Nos. 28303, 28304, and 28305), not only the ground-tissues of the peduncle, but the details of the vascular tissues, are well preserved. The ground-tissue resembles very closely that of the leaf-bases, scales, and other ground-tissue in the plant, and has a large number of the same characteristic "transfusion-tissue" cells ; these show their pits very clearly in many cases, particularly near the circumference of the peduncle in cone Y ; the tissues of the centre, and those of cone X, have suffered in petrifaction.

The presence of gum canals is open to the same doubt as in the case of the bract scale bases.

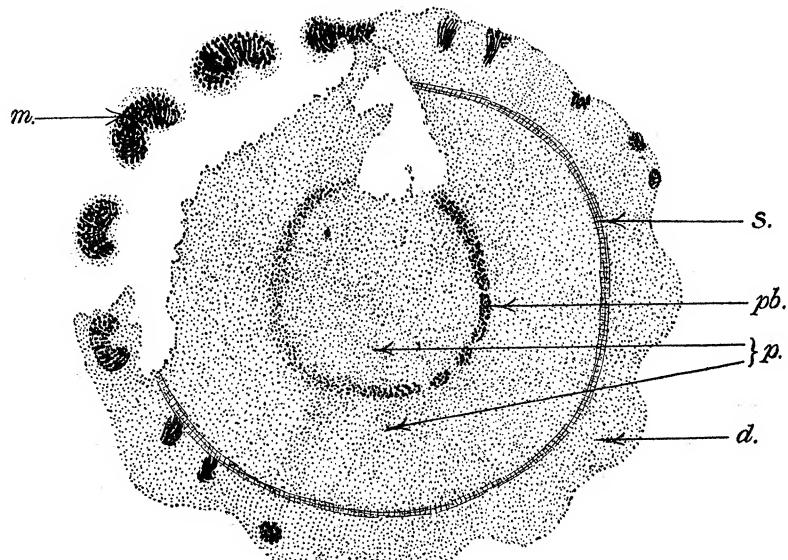
Near the circumference of the peduncle is a slender cylinder of collateral vascular strands (see p, text-fig. 22), from which simple curved arcs go out at frequent intervals to supply the bracts ; one such can be well seen on the left-hand side of the peduncle in text-fig. 22.

These strands, though distinct, are delicate, and the number of xylem elements in radial sequence in them averages only about three to seven.

The sections cease before the lower end of the peduncle has been passed through, so its full extent cannot be determined. It is evident that the peduncle cannot have been less than 12 or 14 mm. in vertical height, and may well have been much more.

THE MALE ORGANS.

Evidence that the cone was bisporangiate, and the male organs were developing at the time the plant was petrified, is to be seen in cone X, Section No. 28299 of which passes through a whorl of structures which must have been the young male organs. This section is nearly transverse, but slightly oblique, so that it cuts the adherent disc on one side and the massive strands separated from it on the other. Unfortunately, this region is rapidly passed through, and the next section above, viz., No. 28298, does not show these structures at all. For their interpretation, therefore, we depend entirely on what can be seen in one section. A photograph of this section is given in Plate 24, fig. 3. A diagrammatic sketch of it is given in text-fig. 23 magnified 12 times. This shows that the peduncle, with its ring of



TEXT-FIG. 23.—*B. maximus*. Diagrammatic sketch of cone X at the level of ♂ organs (*cf.* level *m*, text-fig. 25). *p*, tissues of peduncle; *pb*, ring of developing vascular strands of peduncle; *s*, separation of cork-like cells; *d*, disc tissues; *m*, strands of bases of male of sporophylls (?). [Slide 28299, \times about 12 diameters.]

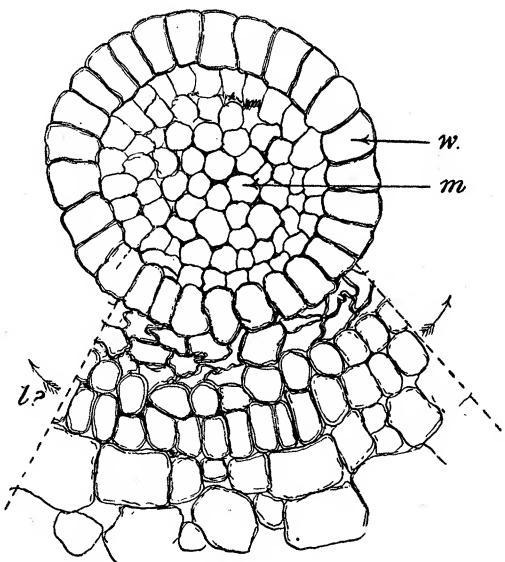
partly developed vascular tissue and meristematic cells, is surrounded by an adherent disc. The demarcation between the tissues is a layer of cork-like cells. The disc or whorl of tissue has a crenulated outer limit, which is not clearly bounded by an epidermis. On the one side, massive curved strands, apparently largely but not entirely composed of meristematic vascular tissue, are separated from the disc and from each other. Individually, they are not surrounded by distinct limiting layers, so it is impossible to determine whether or not they stood actually isolated when living, or were connected by soft tissue, which broke down in the course of petrifaction. I incline to the view that they were connected by soft tissue. Their tissues are all very young, and but partly differentiated within the tissues of the

disc; adjacent on either side to the region of these free strands, several vascular strands can be traced. In the mass of undifferentiated tissue they are not always easy to recognise, hence I cannot feel certain whether there are bundles at the level represented by the lower right-hand side of the disc or not.

The massive meristematic strands *m* (text-fig. 23) appear, from their position and arrangement, to have been 14 in number. They would, presumably, have provided the strands of the central rachis of the individual male sporophylls, and hence have corresponded in number to them. In his restoration of *B. ingens*, WIELAND (1906, Plate 4A) gives 13 male sporophylls springing from the disc, so that the correspondence in the number of the parts between his form and the new immature species is very close. Similarly, 15 is a common number for the male disc of the impressions, called in general *Williamsonia* (see WILLIAMSON, 1868; NATHORST, 1911; WIELAND, 1911, etc.).

The FEMALE RECEPTACLE is so extremely young and undifferentiated that it only amounts to a pad of dense meristematic tissue terminating the peduncle. Through this, in cone X, two sections pass. The section seen in Plate 24, fig. 2, consists of largely undifferentiated tissue in which are a number of small vascular strands, lying mainly in a ring as they come up from the peduncle, but branching and scattered to some extent. They are the strands which would have supplied the ovule-stalks later on, had the plant developed further instead of being petrified.

Section 28297 shows the ovuliferous region of the cone. This is less than 1 mm. larger in diameter than the preceding, and under low magnification appears quite



TEXT-FIG. 24.—*B. maximus*. Outline sketch of transverse section of ovule rudiment and surrounding tissue. Note.—The walls of the cells only are shown and not their dense contents. *w*, limiting layer of ovule, to become the testa?; *m*, central, undifferentiated mass of nucellus; *l*, limiting layer of interseminal scales?

similar to photograph 2, Plate 24. When magnified further, however, the large number of rudimentary ovules scattered through it are apparent. A small sector of this part of the cone is shown in photograph 4, Plate 24, where the circles of the barely differentiated ovules can be seen lying embedded in the dense dark mass of the undifferentiated meristematic tissue (*e.g.*, *o* in fig. 4, and fig. 5, Plate 24). Near the edge, the ovules consist of nothing more than a limiting layer and a central mass of cells, but nearer the centre of the cone the development has gone a little further and two or three layers of the ovule integument are recognisable (see for example *ov* on fig. 6, Plate 24), where the most conspicuous and furthest developed ovule is shown.

At first sight a great many of the extremely young ovules towards the edges of the cone bear a superficial likeness to sporangia, the one limiting layer of the integument superficially resembling an annulus. The central mass of cells from which the nucellus will develop is at this stage entirely undifferentiated. Photographs of such ovules are shown in fig. 5, Plate 24, and in outline sketch in text-fig. 24. In the mass of meristematic tissue in which these ovule rudiments are embedded, there is as yet no clear differentiation of ovule stalk cells or of interseminal scales, but in a few places there seems to be something like the commencement of the limiting layer which would develop later to individualise the interseminal scales (see *l?* text-fig. 24). All these cells are very dense with contents, as can be judged from the photographs in Plate 24.

CONCLUSIONS.

The very slender vascular axis to so large a trunk, and the simple method of branching of the leaf-trace and peduncle strands (described on p. 420), are points of interest in this species. More noteworthy, however, is the apparent lack of gum canals, a lack which does not seem to be merely due to faulty preservation (for, as the photographs on Plates 23 and 24 make clear, the specimen is locally well preserved), but seems to be an inherent characteristic. This may be correlated with the presence of the curious and noticeable cells, the "transfusion-tissue," which forms the most interesting feature of the vegetative parts of the plant. The presence of large "gum canals" is so conspicuous a feature of *Bennettites* that CARRUTHERS (1870) mentioned them as one of the diagnostic characters of the genus. Their absence in the present species is therefore particularly noticeable, and it makes it advisable in future diagnoses of the genus to leave this feature out of the generic and confine it to the specific characters. It is not impossible that the "transfusion" cells may have contained a weak gummy solution and have to some extent performed the function of gum canals. To determine such a point in a fossil, however, is well nigh impossible.

The discovery that this species had *bisporangiate cones* is, of course, the feature of supreme interest in the plant. No other petrified *Bennettites* in this country had

such cones, and, though several suggestions have been made that *B. Gibsonianus*, the famous type, may have been bisporangiate when young, they are based on theoretic deductions, for, in the ovulate cones, which are all we have of the species, no trace of male organs remains. The bisporangiate cones just described are not only the first found in this country, but they are younger, and in an earlier stage of development than any others described. They are of peculiar interest, therefore, as revealing something of the developmental stages of the most intriguing of all fossil fructifications.

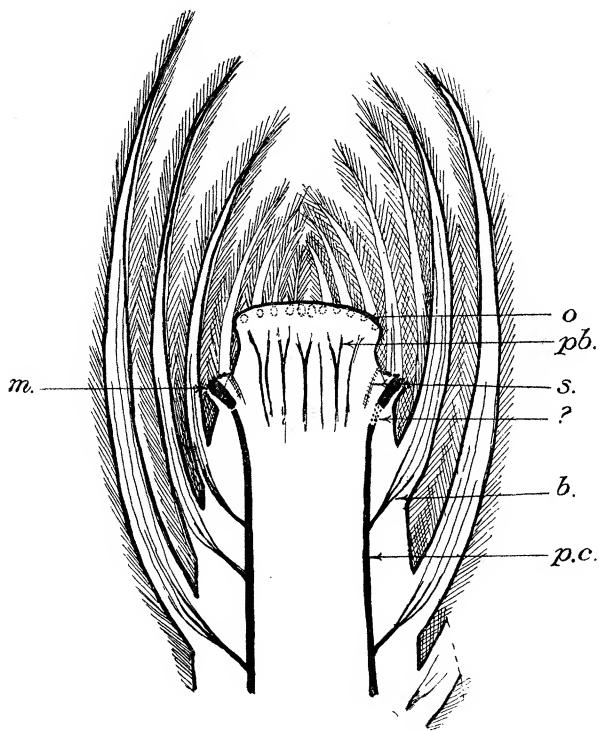
B. maximus and *B. Gibsonianus* being from the same restricted locality and geological horizon, being known only from a single specimen each, and being in such different stages of development, it might be concluded by someone not working on them that they are really the same species. I must emphasise, therefore, the fact that CARRUTHERS undoubtedly was correctly inspired when he, without any examination of the internal parts, diagnosed *B. maximus* as different from *B. Gibsonianus*. The vegetative characters, particularly the absence of gum canals and the presence of the peculiar "transfusion" cells, isolates *B. maximus* vegetatively further from *B. Gibsonianus* than any of the other species of the genus, in all of which gum canals are common.

A detailed comparison of the fruits of these two Lower Greensand species would be very interesting, but, unfortunately, they are too different in age for this to be possible. One can compare with advantage, however, the general proportions of the parts of the cones in these different phases of their development, and to do that I have attempted to give a restoration of the new cone-structures.

As these structures are so small, the ovules, for instance, being passed through only in one section, it is impossible, from the transverse series, to reconstruct an entirely accurate diagram of the arrangement of the whole cone. But, as the essentials are not shown in any of the longitudinal sections, an attempt at such a reconstruction from the sections available has been made. Of both cone X and cone Y 10 transverse sections are available, so that, within limits, the proportions of the parts can be fairly deduced. A diagram, representing the arrangement of the cone in medial longitudinal section, is shown in text-fig. 25. In this will be seen the massive proportions of the peduncle in comparison with the young fertile regions. The contrast between this and the diagrams of the older cones given by WIELAND (1906) (his figs. 56, 71, 79, 87, and others, for instance) is instructive, and the diagrams should be compared, if possible, by the reader. The proportions of the parts of the present extremely young cone fully bears out WIELAND'S deduction (1906, p. 178) that, in their development, the "early growth of the peduncles to a nearly normal length and size took place before any well-marked strobilar development."

It is, of course, impossible to be quite certain from the material available what stage of development was reached by the male organs, but it seems likely that the

massive strands represented by *m* in text-figs. 23 and 25 entered still unfolded rudiments, for, in the sections above this level, there is no sign of either the male



TEXT-FIG. 25.—*B. maximus*. Restoration of extremely young cone. *pc*, peduncle cylinder; *b*, meristeles therefrom breaking up as they pass into the bracts; *m*, large strands passing out to male sporophylls; *pb*, ring of bundles in base of ovuliferous cone; *s*, zone of corky cells separating ♂ disc from central tissues; *o*, apex of cone, ovuliferous region with developing ovule rudiments. Note.—Slide 28299, text-fig. 23, passes through level *m* very slightly obliquely.

structures or the appropriate spaces in which they might have lain had they been developed and disintegrated before or during petrification.

BENNETTITES MAXIMUS, CAR.

- 1870. *Bennettites maximus*, CARRUTHERS, 'Trans. Linn. Soc.', vol. 26, p. 699.
- 1887. *Bennettites maximus*, SOLMS-LAUBACH, 'Einleit. Paläophytol.', p. 100.
- 1891. *Bennettites maximus*, SOLMS-LAUBACH, 'Ann. Bot.', vol. 5, p. 432.
- 1906. *Bennettites maximus*, WIELAND, 'American Fossil Cycads', p. 19.
- 1915. *Bennettites maximus*, STOPES, 'Brit. Mus. Cat. Cretaceous Flora', vol. 2, pp. 50–53, text-fig. 14.

Only the one specimen of this species, that diagnosed by CARRUTHERS in 1870, is known. But I have a suspicion that a second specimen of the same or a closely allied species is in existence somewhere and has been confused with and included under *B. Saxbyanus*. The reason for this is that, when, for comparative purposes, I was studying the slides of the latter species in the British Museum, I noticed that three slides of those recorded as *B. Saxbyanus* differed markedly from the others. Unfortunately all these slides were transferred from the Botanical Department too

late to be considered in SEWARD'S 'Catalogue of the Wealden Flora,' and they are without any history. The slides include one transverse and two radial sections (Nos. V. 8407, transverse, V. 8405, and V. 8408) in the Geological Dept., Brit. Mus. Nat. Hist., and their tissues are fairly well preserved. In this specimen, as in *B. maximus*, no gum canals are recognisable, but a great many pitted cells are present in the pith and elsewhere which are identical with the peculiar cells described for *B. maximus* (see text-fig. 21, p. 423) and the like of which I know in no other species of the family. These sections are evidently very old, and it is possible that others of the same type may be in some other collections, and that anyone working on the group in other collections might come across further sections, or the block from which they were cut, and which would yield new sections. In that case the establishment of a second specimen of this interesting species may be anticipated.

Diagnosis: Trunk $22 \times ?$ cm. high, 30×17 cm. in diameter (the elliptical compression apparently natural). Pith 14.5×7 cm. in diameter, apparently without gum canals; numerous large pitted "transfusion cells" scattered all through it, but no vascular strands. Vascular cylinder of axis exceedingly slender, with a single cambium giving rise to secondary tissues. In the middle of the trunk the xylem only 2 mm., and the phloem 4 mm., in radial thickness; at the lower end of the trunk the xylem 3–4 mm. and the phloem 6–7 mm. thick. Wood entirely centrifugal; tracheids up to $50\ \mu$ in diameter, all with scalariform pitting. Phloem with single thin elements and fibres alternating on the same radius. Medullary rays principally uniseriate; ray cells with irregular pits on the radial walls where crossing the tracheids, with some irregular pitted areas in the phloem. Leaf-bases irregularly rhomboidal, according to position, 2–4 cm. in tangential, and 1–1.5 cm. in vertical diameter. Areas of surrounding ramenta very extensive. Vascular bundles with entirely centrifugal xylem. In the ground tissue large numbers of large, pitted "transfusion cells." Cones numerous, about 1 cm. apart. Bisporangiate. In the very young stage in which they are preserved the peduncle well developed, while the fertile region is still meristematic. Characteristic "transfusion cells" in the peduncle and bracts. Segments of ♂ organs, 14. Meristematic ♀ cone terminal, in which the earliest recognisable state of the ovules is a central mass of cells with a single relatively large limiting layer.

Horizon: Lower Greensand.

Locality: Isle of Wight.

Type: And only specimen: A large trunk in the Museum of Practical Geology, Jermyn Street, London. Registered No. 27034. And sections from it, viz., 9 of the trunk and 11 of cones and leaf-bases, Nos. 28286–28305. (Nos. V. 8407, 8405, and 1408, Brit. Mus. Nat. Hist., possibly sections from a second specimen.)

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DESCRIPTION OF PLATES.

Of the following photographs, the series 1–5, Plate 19, were taken by Mr. LOMAX; figs. 1–2, Plate 23, and figs. 1–3, Plate 24, by Mr. BARLOW of the British Museum. The rest were taken by the author.

PLATE 19.

Bennettites albianus, sp. nov.

Figs. 1–5 are in series, corresponding to slides A–G (see text-fig. 1), and are all on the same scale of magnification, viz., about 2 diams. In all these figures, *st* is the stalk region, the stalks being cut in transverse section; *b*, the bases of the seeds; *s*, seeds at various levels; *a*, apices of the seeds; *m*, the micropyles and surrounding interseminal scales.

Fig. 1.—Nearly all stalks, with a few seeds on the right-hand side.

Figs. 2 and 3.—Seeds and stalks.

Figs. 4 and 5.—Seeds only.

Note, particularly in figs. 3, 4 and 5, how many of the seeds show embryos even in this low scale of magnification.

Fig. 6.—Enlargement of level of free micropyle, and the rounding off of the terminations of the interseminal scales. This is from about the same level as fig. 1, Plate 20; *m*, lining of micropyle (cf. also Plate 22, fig. 3); *pl*, plastid layer bounding the outer limit of scales; *s*, stone-cell region of scales.

Fig. 7.—Transverse section of small part of basal region of a seed at a level corresponding to or a little below that shown on Plate 20, fig. 10; *n*, nucellus; *b*, broken space between nucellus and integument; lettering as for fig. 8.

Fig. 8.—Transverse section of part of integument at middle of seed: *i*, cells of inner, thin-walled layer of integument; *ms*, middle stone cells or fibrous layer; *os*, outer stone cells; *d*, deliquescent layer, broken down; *t*, tubular cells of "cupule" like extensions of stalk; *f*, fungal spore; *ep*, epidermis of surrounding interseminal scale.

PLATE 20.

All *B. albianus*, sp. nov.

NOTE.—This whole Plate, and Plate 3, figs. 11–15, show different levels of the seed, from different individuals but all on exactly the same scale of magnification, and in series from the apex to the base. \times approximately 40 diameters.

Fig. 1.—*m*, micropyle surrounded by the rounding-off terminations of interseminal scales; *iv*, central vascular strand of interseminal scale; *pl*, plastid-epidermis bounding each interseminal scale. [Slide C.]

Fig. 2.—Central micropyle, lower down, plugged with nucellar tissue. At this region the surrounding interseminal scales are fused; *s*, stone cells of scale ground tissue; *iv*, central vascular strand of each scale. [Slide F.]

Fig. 3.—The region of the seed where the micropyle is merging with the ribbed apex of the neck of the seed-coat proper, at the same time its ribs are practically merged with the tissues of adjacent scales. The central plug of tissue is to be seen in the micropyle. [Slide G.]

Fig. 4.—The stone of the five-ribbed seed-coat, clearly differentiated from the surrounding stone cells of the scales. The last of the nucellar plug of the micropyle can be seen in the centre. [Slide G.]

Fig. 5.—The five-ribbed shoulder of the seed, showing the differentiation of the stone cells of the corners. In the central space of the seed the shrivelled and corrugated radicle of the embryo can be seen. Note the hard, stony tissues of the surrounding interseminal scales.

Fig. 6.—Another section from almost the same level as fig. 5. The bounding layers of the interseminal scales are clear. [Slide G.]

Fig. 7.—Section approaching the middle region of the seed. The ribs have entirely died out, and the seed-coat is nearly circular and smooth. The large hypocotyl region of the embryo bulks conspicuously in the centre, and its flat vascular strand can be recognised. [Slide E.]

Fig. 8.—A similar section, from the largest diameter of the seed. At the corners of the photograph portions of its four neighbours are visible and show how closely the seeds approximate in this region. [Slide G.]

Fig. 9.—A similar section, somewhat lower down in the seed, showing portions of six neighbouring seeds. The central seed has a well-preserved embryo in which the two cotyledons are well preserved. [Slide F.]

Fig. 10.—Section near the base of the seed, on the right side the details of the integument can be well seen; *t*, the tubular cells of the "cupule" like extension of the stalk which surround the seed; *ep*, limiting epidermis of interseminal scales. [Slide C.]

PLATE 21.

(Series on Plate 20 *continued.*)

Fig. 11.—Section from the base of the seed; *int*, integument. Within this, separated from it by a space, is the nucellus, *n*; *t*, tubular cells of the "cupule"; *ep*, epidermis of interseminal scales; *s*, stone cells of the same.

Fig. 12.—Extreme base of seed; vascular strand entering the centre of the integument. The section has a trifling obliquity.

- Fig. 13.—Ultimate base of the seed; vascular strand with two or three stone cells round it. Note the large-celled tubular cupule. [Slide D.]
- Fig. 14.—Stalk region, below seed-bases. Note the interseminal scales with vascular strands and resin canals, *r*; *t*, tubular cells of seed stalks. [Slide A.]
- Fig. 15.—Seed stalk some distance below seed. The tubular cells of the seed stalk *t* should be compared with the same cells in fig. 13. These two photographs were taken without moving the camera and the magnification is therefore identical. [Slide A.]
- Fig. 16.—A large scale view of the terminations of the interseminal scales, and their "plastid" epidermis. This is from a level corresponding to fig. 1, Plate 20. [Slide C.]
- Fig. 17.—A larger scale view of a seed very slightly below that in fig. 6, Plate 20. On the left the darker walls of the corner stone cells stand out clearly. This should be compared with text-fig. 9. [Slide F.]
- Fig. 18.—A larger scale view of the base of the micropyle, just joining on to the ribbed top of the seed; this is from the same level as fig. 3, Plate 20; *iv*, central strands of the interseminal scales which are largely fused in this region. [Slide G.]

PLATE 22.

All *Bennettites albianus*, sp. nov.

- Fig. 1.—Enlarged view of part of the tissue of the interseminal scale, as shown in fig. 14, Plate 21; *ep*, epidermis of scale; *iv*, vascular strand; *r*, resin canals. Text-fig. 3 should be compared. [Slide A.]
- Fig. 2.—Enlargement of the tubular epidermal cells, *t*, of the seed stalks shown in Plate 21, fig. 15; *ep*, epidermis of adjacent interseminal scales. [Slide A.]
- Fig. 3.—Enlarged view of the cells of the micropyle, very slightly oblique: *mei*, inner layer of micropyle epidermis; *mo*, outer, thick-walled stone cells; *mn*, nucellar plug of micropyle. [Slide F.]
- Fig. 4.—Enlargement of the ribbed apex of the seed, from a transverse section immediately below the level of fig. 4, Plate 20. The groups of dark cells at the five corners can be seen, cf. text-fig. 9. The outer stone layer of the seed is distinct from but not yet fully separated from the surrounding layers of the scales and the fragments of the deliquescent layer; *cy*, contents-containing cells, cf. text-figs. 6 and 11. [Slide G.]
- Fig. 5.—Transverse section of seed with embryo: *os*, cells of outer stone of seed integument; *t*, tubular "cupule" cells; in the embryo the two large cotyledons, with a row of vascular strands in each, are conspicuous; *o*, other adjacent seeds; *i*, interseminal scale tissues.

PLATE 23.

Bennettites maximus, CARR.

Fig. 1.—Transverse section of a part of the main trunk, showing the central vascular cylinder with outgoing leaf-traces, and the large areas of ramenta surrounding the young cones and leaf-bases: *p*, pith; *x*, xylem of central cylinder, the white streak running tangentially separates it from the phloem, *ph*; *lb*, leaf-base, cut somewhat obliquely; *lt*, leaf-trace; *c*, obliquely cut cone, surrounded by its scales cut in various directions; *r*, ramenta. (Sect. No. 28293. \times about $1\frac{1}{2}$ diam.)

Fig. 2.—Radial longitudinal section of trunk corresponding to transverse Section 1. Lettering the same as above. Note particularly the outgoing strand *a*, and the way it breaks up in a spraying manner to several strands almost simultaneously at *s*. This should be compared with text-fig. 18. (Section No. 28291. \times about $1\frac{1}{3}$ diam.)

Fig. 3.—Transverse section of the ground-tissue and a vascular bundle of a leaf-base. Note the thick-walled, pitted cells of the bundle sheath all round the vascular strand *st*, and the larger cells of the same type thickly scattered through the ground tissue *t*. Compare with text-fig. 21.

Fig. 4.—Small portion of ground tissue as in fig. 3, enlarged to show the pitted transfusion elements *t*. Note that the pits are in definite areas.

PLATE 24.

Figs. 1, 2 and 3 almost magnified 1·5 diameters.

Fig. 1.—Transverse section of the top of Cone X with surrounding ramenta, leaf-base *lb*, and parts of other cones and leaf-bases. [Slide 28296.]

Fig. 2.—Cone X cut in the ovulate region. Note the dense meristematic tissues. On the right the scales of Cone Y are seen. [Slide 28298.]

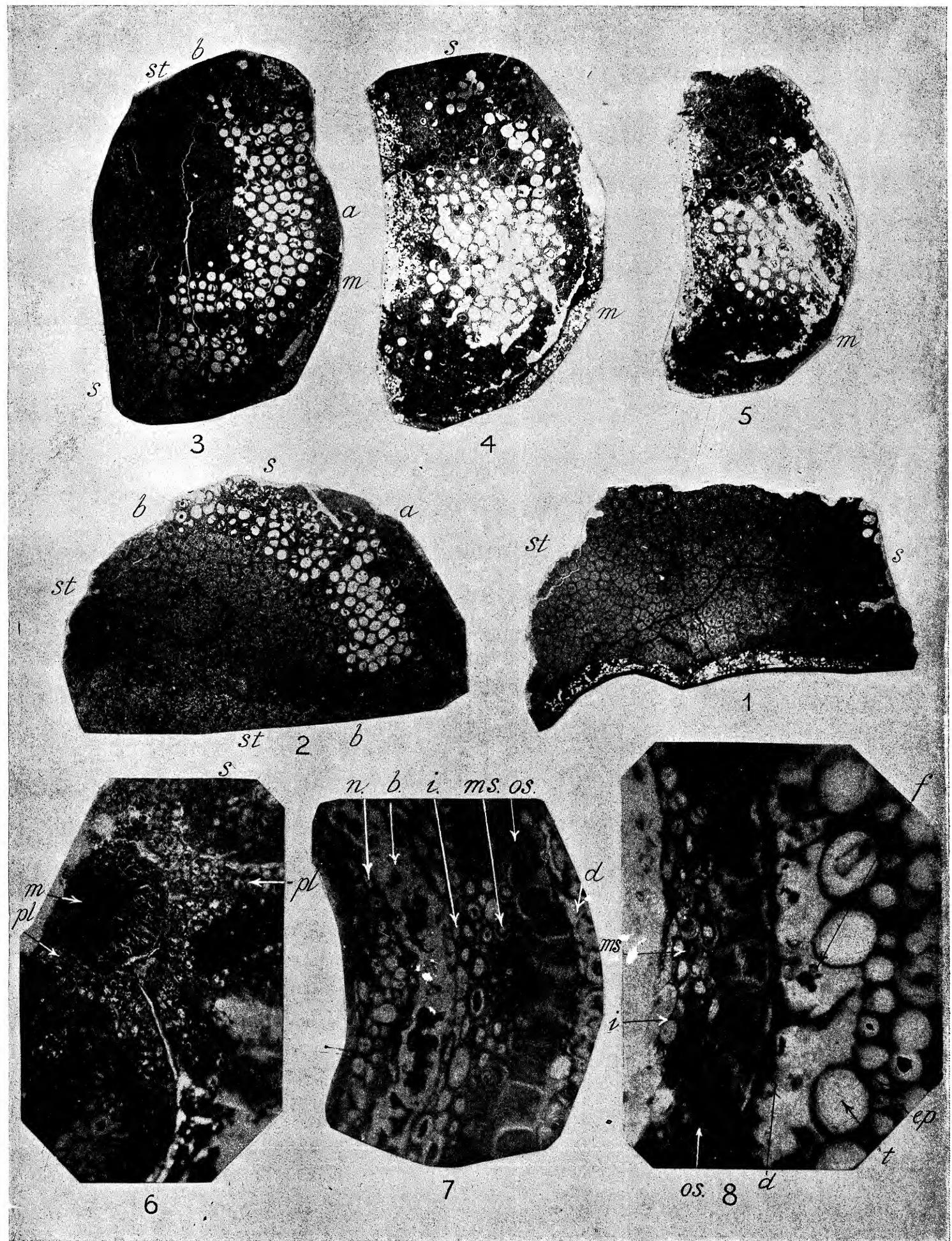
Fig. 3.—Cone X cut in region of ♂ disc. Cone Y seen on the right. [Slide 28299.]

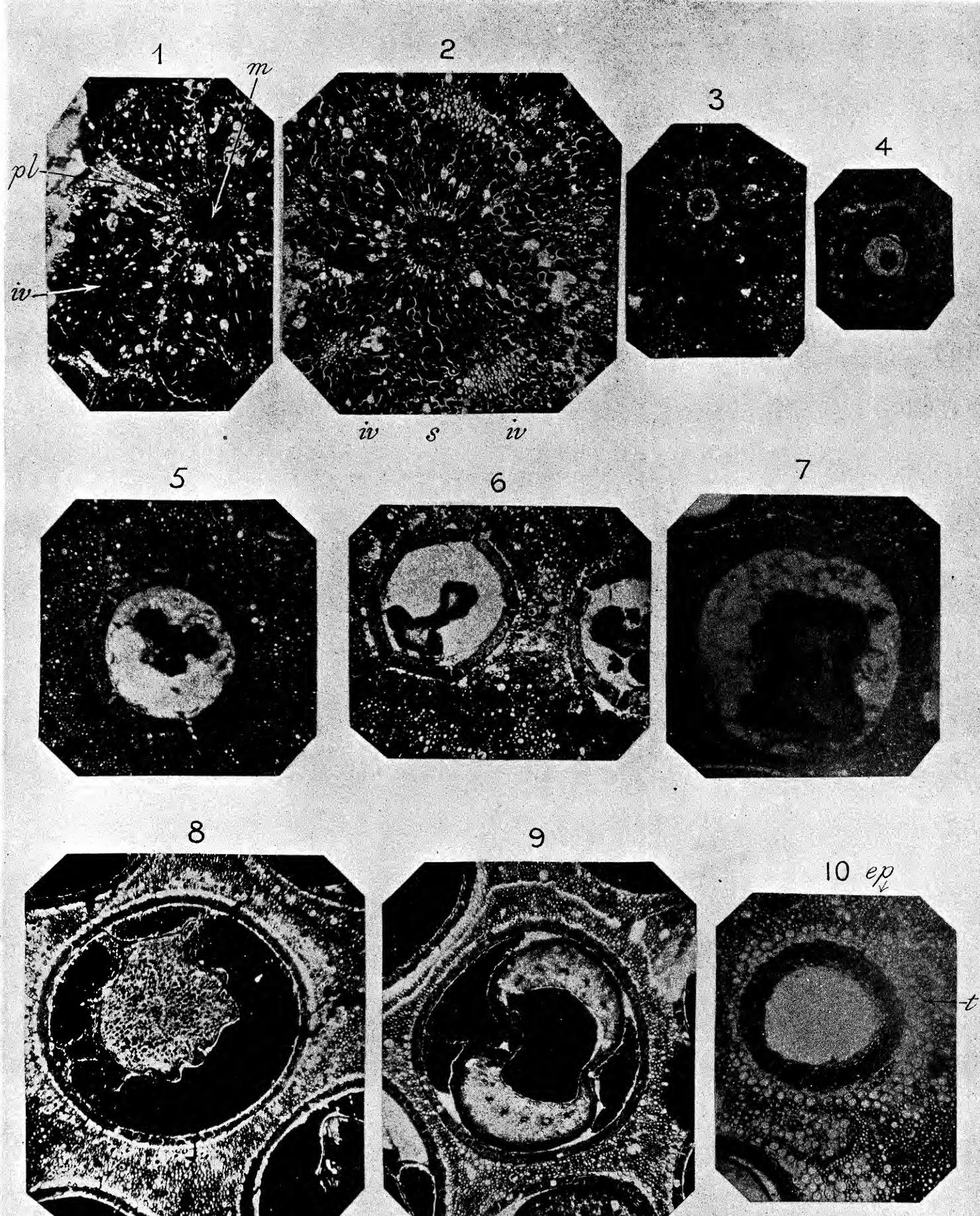
Fig. 4.—The edge of Cone X further enlarged, showing the developing ovules *o*. [Slide 28297.]

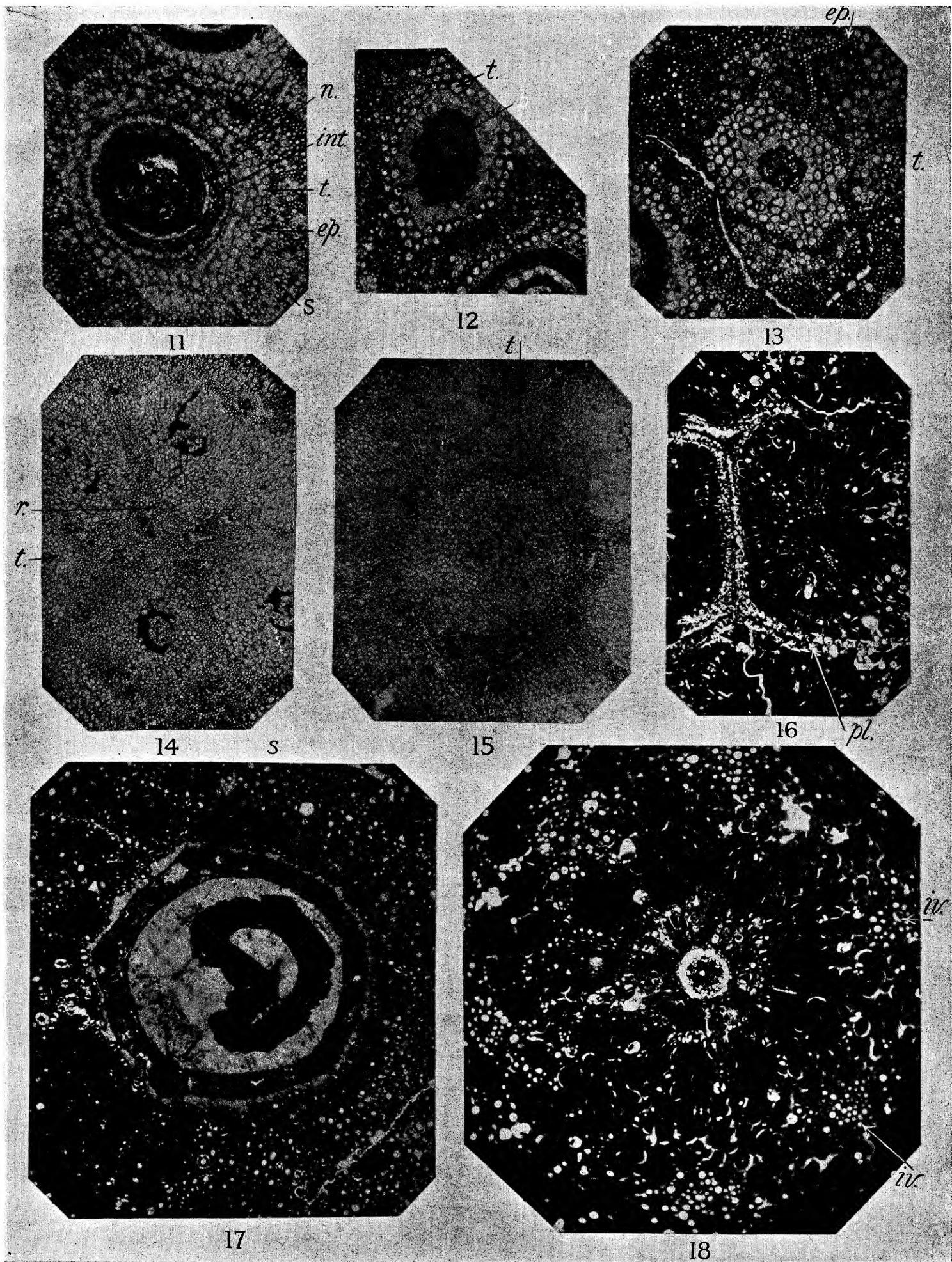
Fig. 5.—Another portion of the same further magnified; *o*, ovules, in which the limiting layer and the solid central mass can be distinguished. [Slide 28297.]

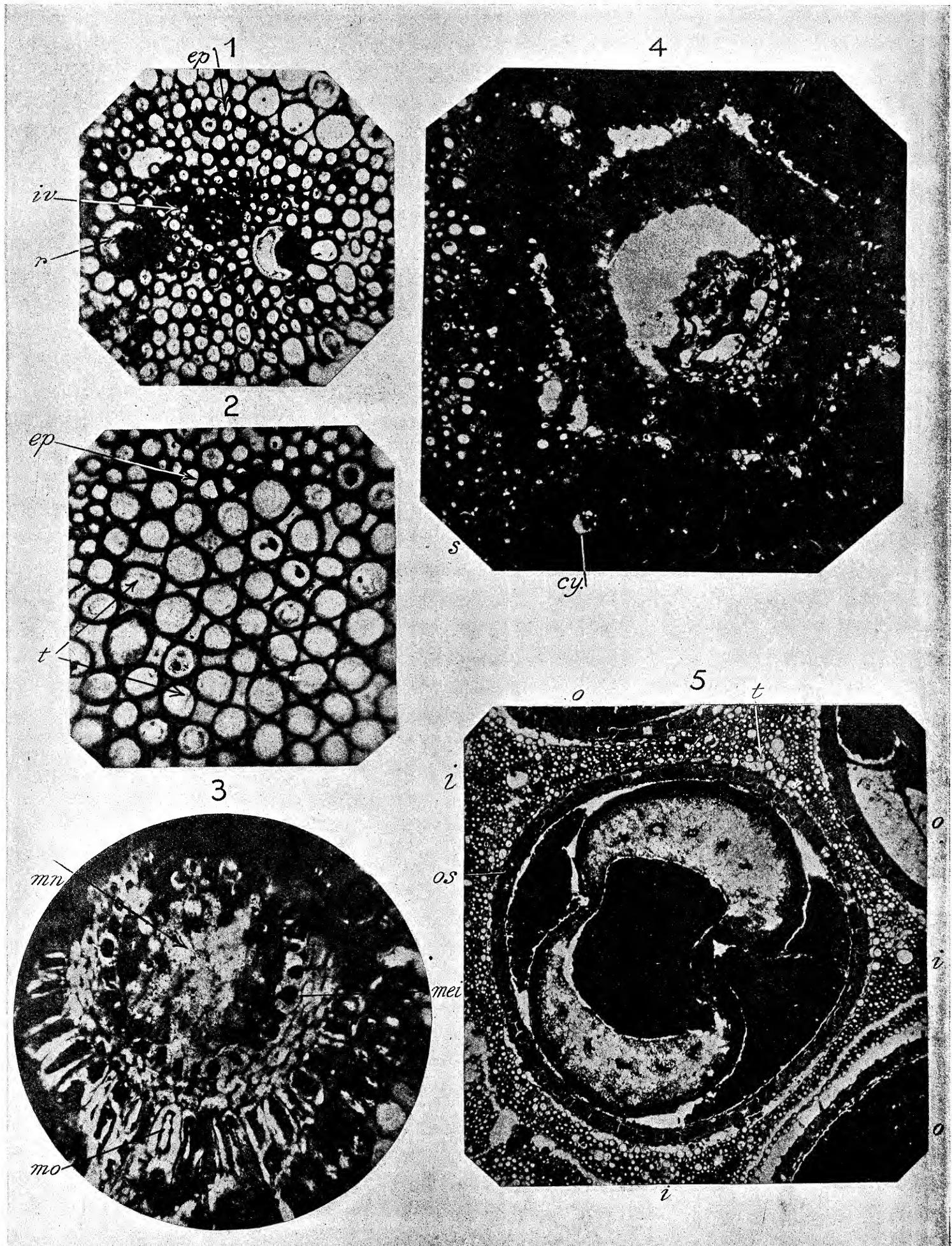
Fig. 6.—Central portion of the same cone section as shown in figs. 4 and 5, showing a central ovule more developed than the others, *ov*. It is surrounded by a number of other, less perfect ones, *o*.

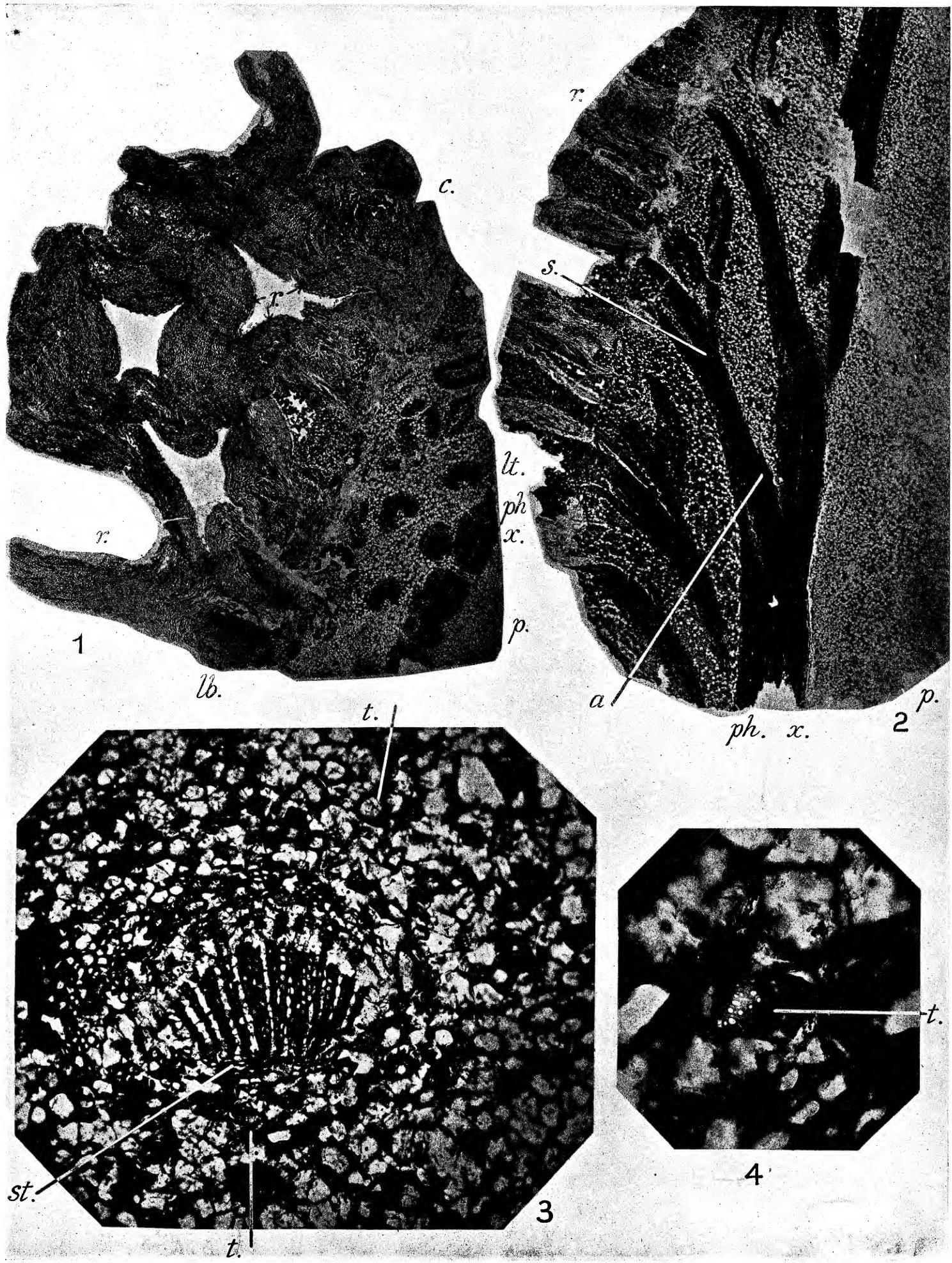
Fig. 7.—Portion of the vascular cylinder of the main axis: *p*, pith; *px*, protoxylem; *x*, centrifugal xylem; *ph*, phloem. [Slide 28293.]

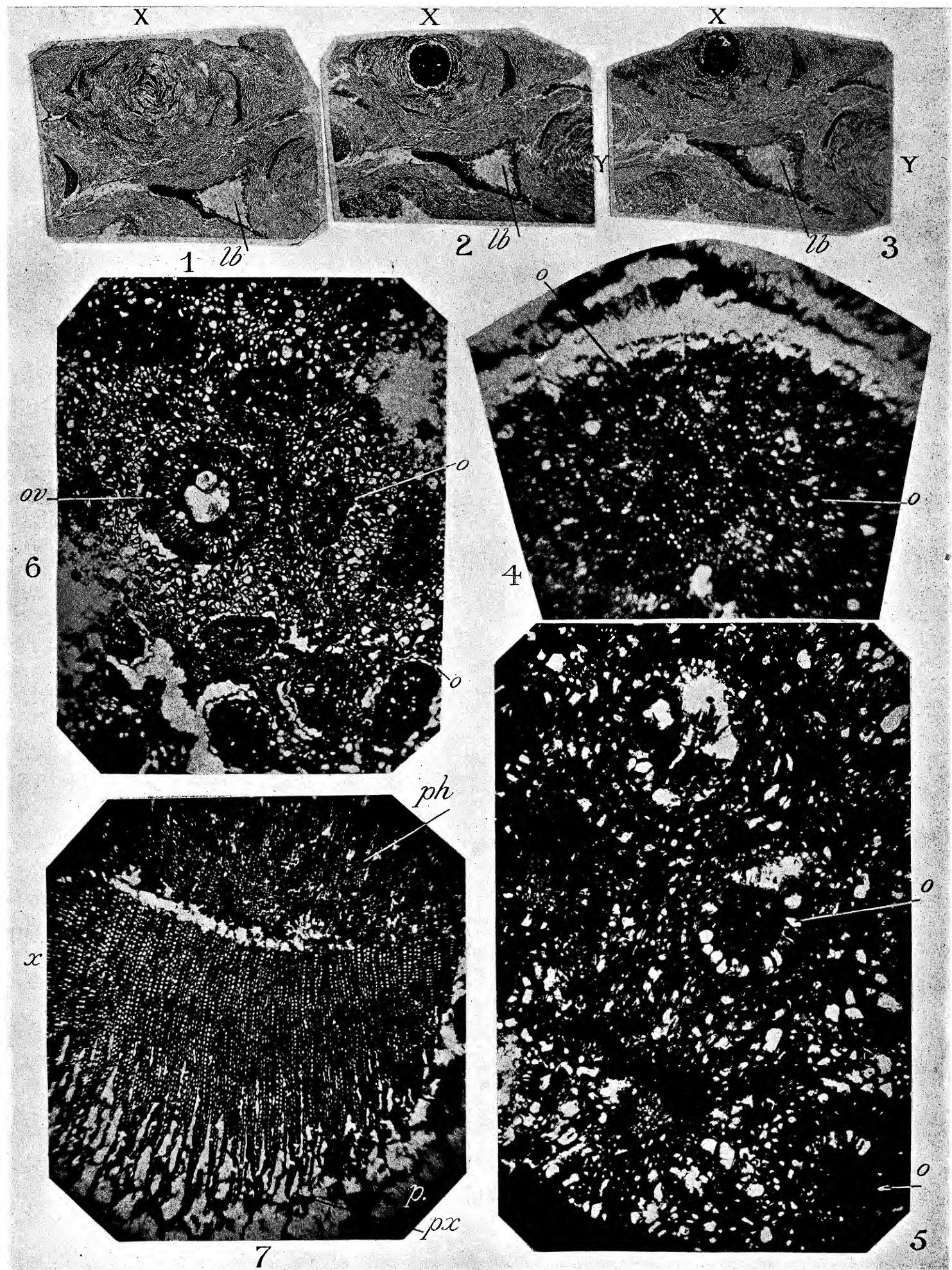












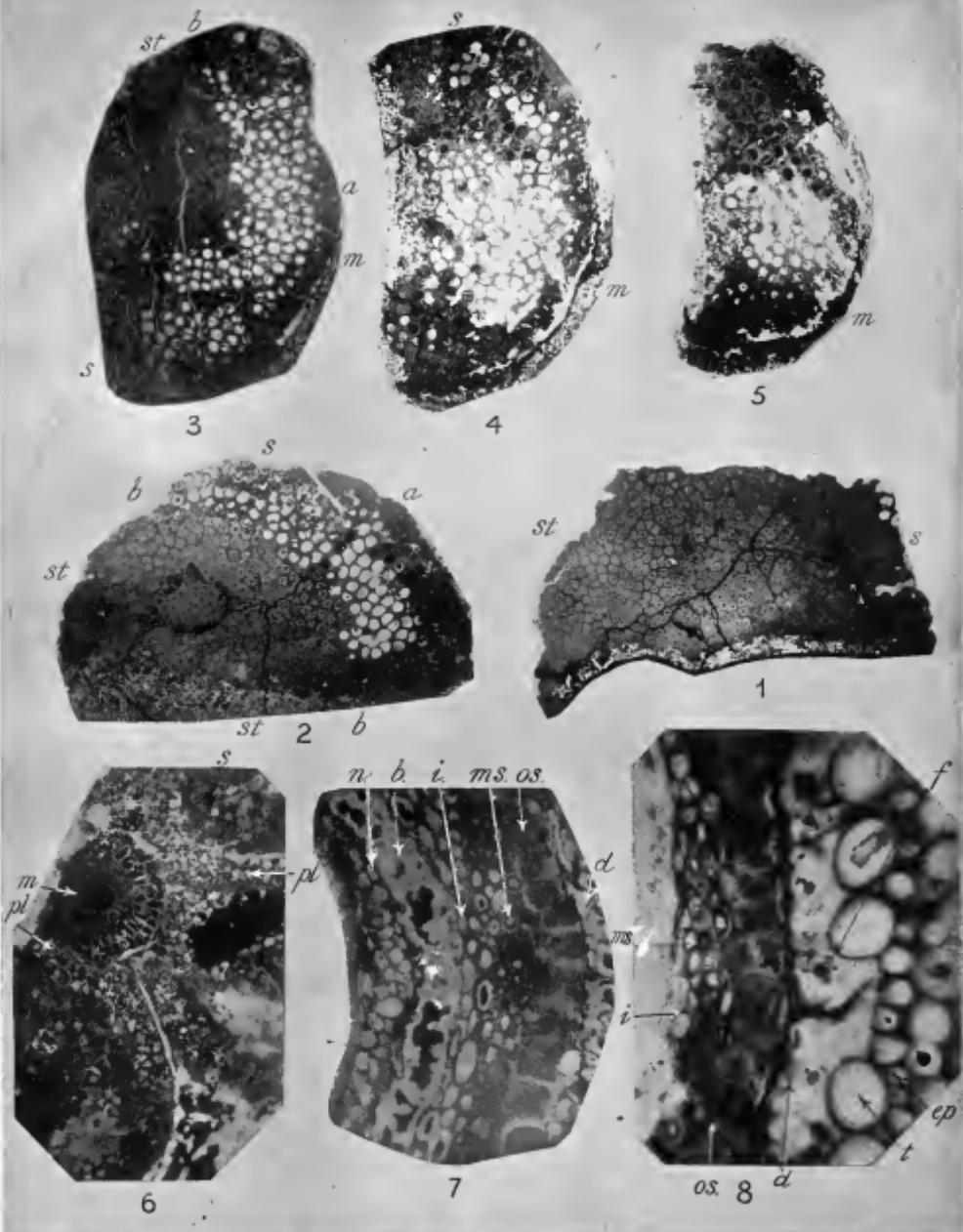


PLATE 19.

Bennettites albianus, sp. nov.

Figs. 1-5 are in series, corresponding to slides A-G (see text-fig. 1), and are all on the same scale of magnification, viz., about 2 diams. In all these figures, *st* is the stalk region, the stalks being cut in transverse section; *b*, the bases of the seeds; *s*, seeds at various levels; *a*, apices of the seeds; *m*, the micropyles and surrounding interseminal scales.

Fig. 1.—Nearly all stalks, with a few seeds on the right-hand side.

Figs. 2 and 3.—Seeds and stalks.

Figs. 4 and 5.—Seeds only.

Note, particularly in figs. 3, 4 and 5, how many of the seeds show embryos even in this low scale of magnification.

Fig. 6.—Enlargement of level of free micropyle, and the rounding off of the terminations of the interseminal scales. This is from about the same level as fig. 1, Plate 20; *m*, lining of micropyle (cf. also Plate 22, fig. 3); *pl*, plastid layer bounding the outer limit of scales; *s*, stone-cell region of scales.

Fig. 7.—Transverse section of small part of basal region of a seed at a level corresponding to or a little below that shown on Plate 20, fig. 10; *n*, nucellus; *b*, broken space between nucellus and integument; lettering as for fig. 8.

Fig. 8.—Transverse section of part of integument at middle of seed: *i*, cells of inner, thin-walled layer of integument; *ms*, middle stone cells or fibrous layer; *os*, outer stone cells; *d*, deliquescent layer, broken down; *t*, tubular cells of "cupule" like extensions of stalk; *f*, fungal spore; *ep*, epidermis of surrounding interseminal scale.

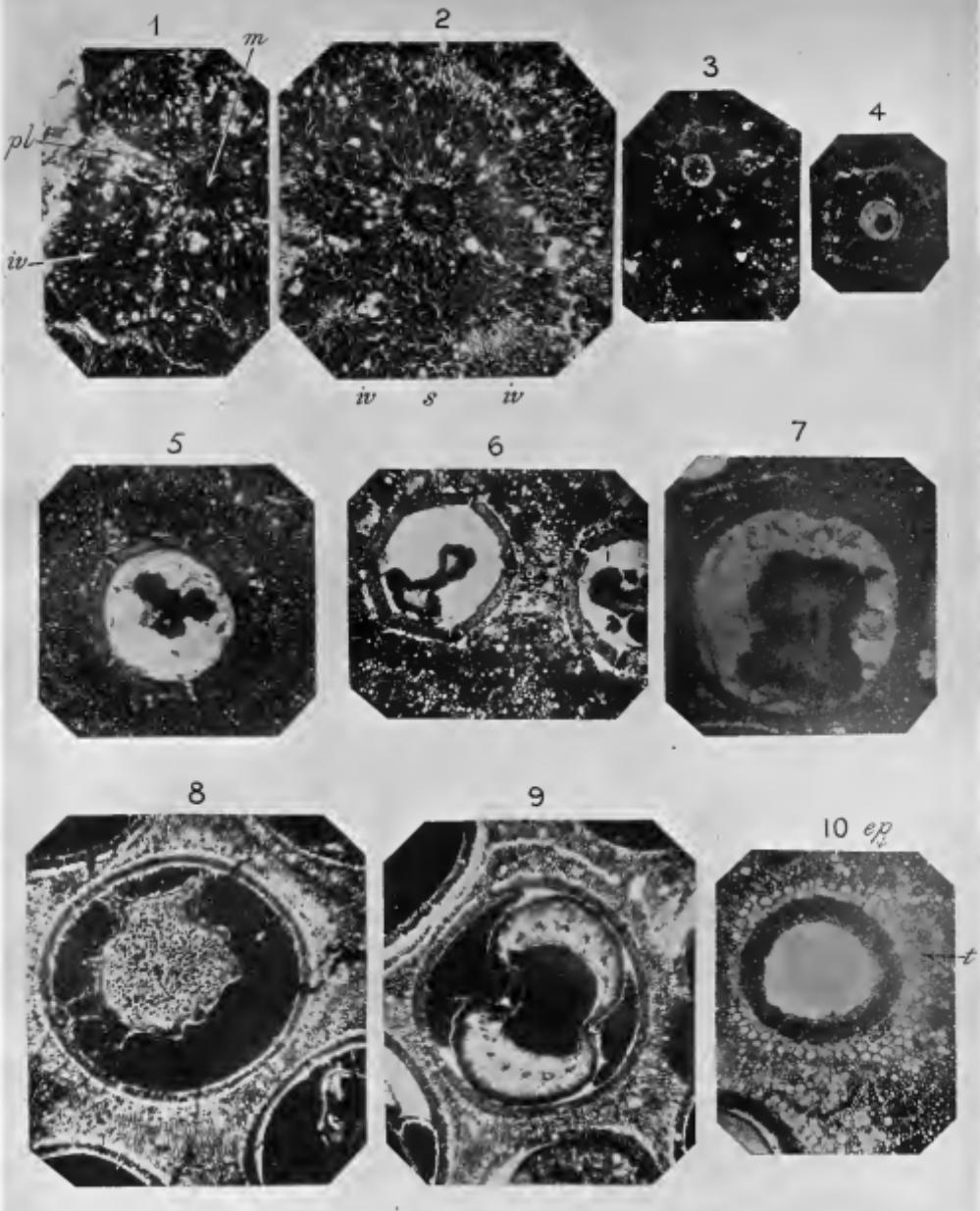


PLATE 20.

All *B. albianus*, sp. nov.

NOTE.—This whole Plate, and Plate 3, figs. 11–15, show different levels of the seed, from different individuals but all on exactly the same scale of magnification, and in series from the apex to the base. \times approximately 40 diameters.

Fig. 1.—*m*, micropyle surrounded by the rounding-off terminations of interseminal scales; *iv*, central vascular strand of interseminal scale; *pl*, plastid-epidermis bounding each interseminal scale. [Slide C.]

Fig. 2.—Central micropyle, lower down, plugged with nucellar tissue. At this region the surrounding interseminal scales are fused; *s*, stone cells of scale ground tissue; *iv*, central vascular strand of each scale. [Slide F.]

Fig. 3.—The region of the seed where the micropyle is merging with the ribbed apex of the neck of the seed-coat proper, at the same time its ribs are practically merged with the tissues of adjacent scales. The central plug of tissue is to be seen in the micropyle. [Slide G.]

Fig. 4.—The stone of the five-ribbed seed-coat, clearly differentiated from the surrounding stone cells of the scales. The last of the nucellar plug of the micropyle can be seen in the centre. [Slide G.]

Fig. 5.—The five-ribbed shoulder of the seed, showing the differentiation of the stone cells of the corners. In the central space of the seed the shrivelled and corrugated radicle of the embryo can be seen. Note the hard, stony tissues of the surrounding interseminal scales.

Fig. 6.—Another section from almost the same level as fig. 5. The bounding layers of the interseminal scales are clear. [Slide G.]

Fig. 7.—Section approaching the middle region of the seed. The ribs have entirely died out, and the seed-coat is nearly circular and smooth. The large hypocotyl region of the embryo bulks conspicuously in the centre, and its flat vascular strand can be recognised. [Slide E.]

Fig. 8.—A similar section, from the largest diameter of the seed. At the corners of the photograph portions of its four neighbours are visible and show how closely the seeds approximate in this region. [Slide G.]

Fig. 9.—A similar section, somewhat lower down in the seed, showing portions of six neighbouring seeds. The central seed has a well-preserved embryo in which the two cotyledons are well preserved. [Slide F.]

Fig. 10.—Section near the base of the seed, on the right side the details of the integument can be well seen; *t*, the tubular cells of the "cupule" like extension of the stalk which surround the seed; *ep*, limiting epidermis of interseminal scales. [Slide C.]

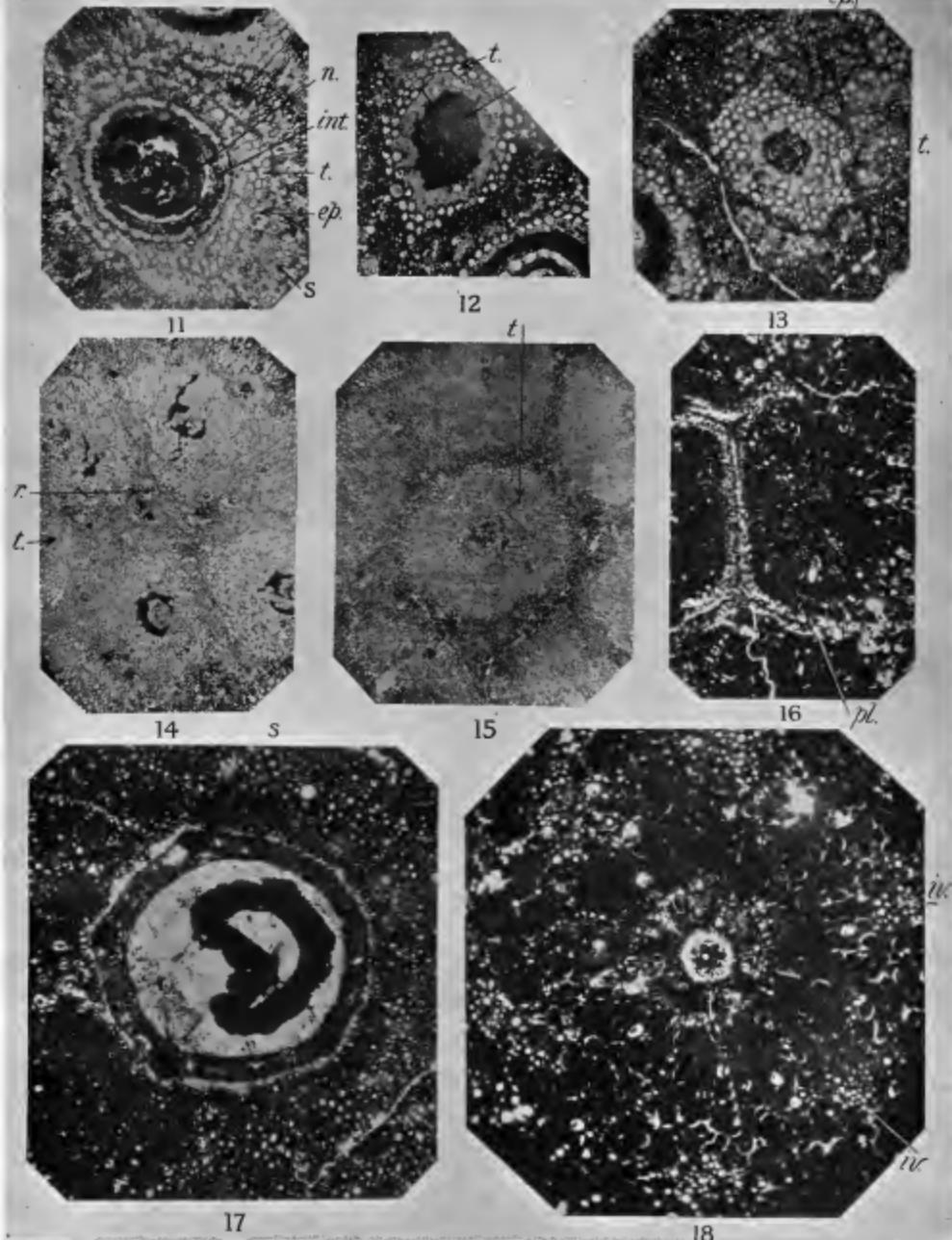


PLATE 21.

(Series on Plate 20 continued.)

Fig. 11.—Section from the base of the seed; *int.*, integument. Within this, separated from it by a space, is the nucellus, *n*; *t*, tubular cells of the "cupule"; *ep.*, epidermis of interseminal scales; *s*, stone cells of the same.

Fig. 12.—Extreme base of seed; vascular strand entering the centre of the integument. The section has a trifling obliquity.

Fig. 13.—Ultimate base of the seed; vascular strand with two or three stone cells round it. Note the large-celled tubular cupule. [Slide D.]

Fig. 14.—Stalk region, below seed-bases. Note the interseminal scales with vascular strands and resin canals, *r*; *t*, tubular cells of seed stalks. [Slide A.]

Fig. 15.—Seed stalk some distance below seed. The tubular cells of the seed stalk *t* should be compared with the same cells in fig. 13. These two photographs were taken without moving the camera and the magnification is therefore identical. [Slide A.]

Fig. 16.—A large scale view of the terminations of the interseminal scales, and their "plastid" epidermis. This is from a level corresponding to fig. 1, Plate 20. [Slide C.]

Fig. 17.—A larger scale view of a seed very slightly below that in fig. 6, Plate 20. On the left the darker walls of the corner stone cells stand out clearly. This should be compared with text-fig. 9. [Slide F.]

Fig. 18.—A larger scale view of the base of the micropyle, just joining on to the ribbed top of the seed; this is from the same level as fig. 3, Plate 20; *iv*, central strands of the interseminal scales which are largely fused in this region. [Slide G.]

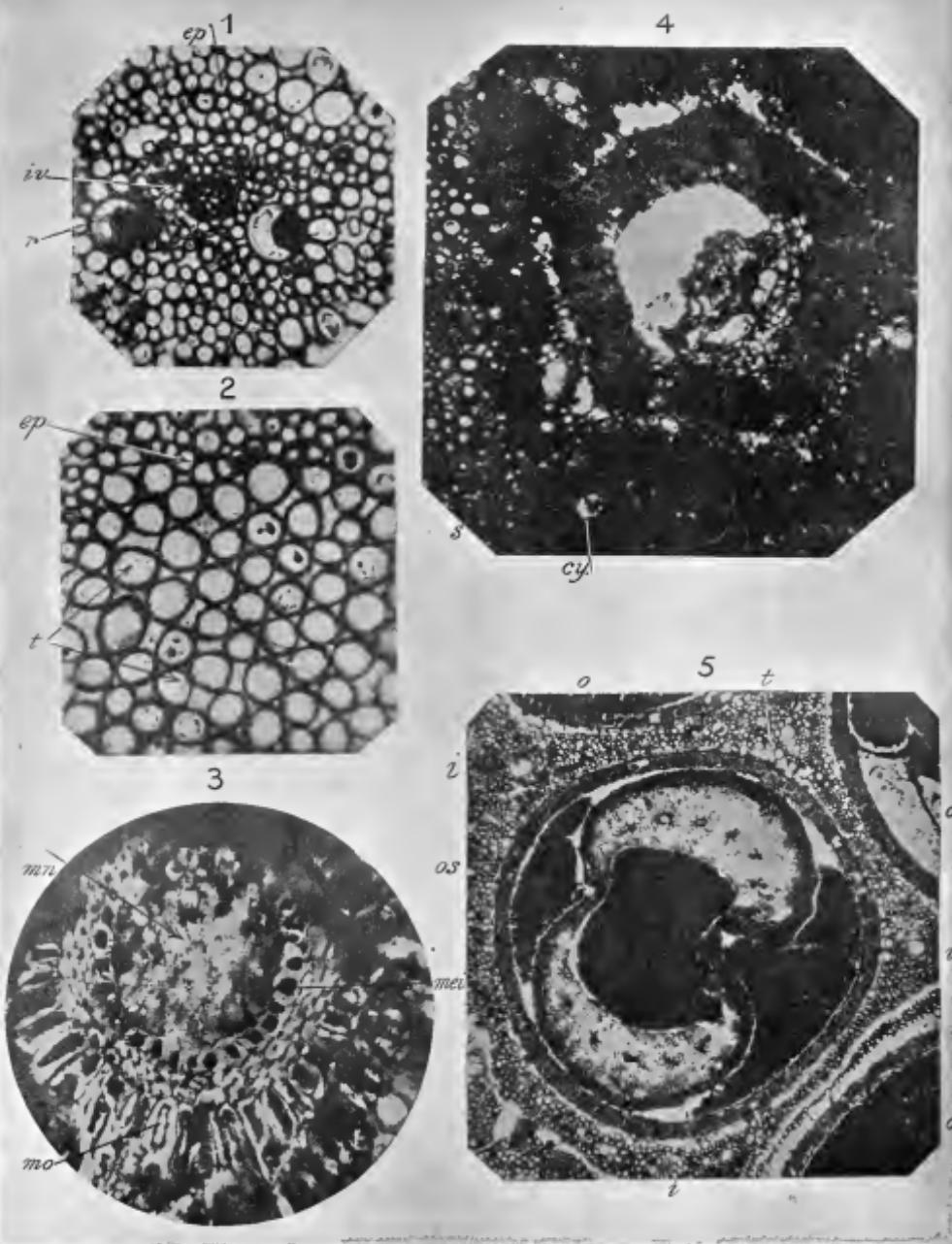


PLATE 22.

All *Bennettites albianus*, sp. nov.

Fig. 1.—Enlarged view of part of the tissue of the interseminal scale, as shown in fig. 14, Plate 21; *ep*, epidermis of scale; *iv*, vascular strand; *r*, resin canals. Text-fig. 3 should be compared. [Slide A.]

Fig. 2.—Enlargement of the tubular epidermal cells, *t*, of the seed stalks shown in Plate 21, fig. 15; *ep*, epidermis of adjacent interseminal scales. [Slide A.]

Fig. 3.—Enlarged view of the cells of the micropyle, very slightly oblique: *mei*, inner layer of micropyle epidermis; *mo*, outer, thick-walled stone cells; *mn*, nucellar plug of micropyle. [Slide F.]

Fig. 4.—Enlargement of the ribbed apex of the seed, from a transverse section immediately below the level of fig. 4, Plate 20. The groups of dark cells at the five corners can be seen, cf. text-fig. 9. The outer stone layer of the seed is distinct from but not yet fully separated from the surrounding layers of the scales and the fragments of the deliquescent layer; *cy*, contents-containing cells, cf. text-figs. 6 and 11. [Slide G.]

Fig. 5.—Transverse section of seed with embryo: *os*, cells of outer stone of seed integument; *t*, tubular "cupule" cells; in the embryo the two large cotyledons, with a row of vascular strands in each, are conspicuous; *o*, other adjacent seeds; *i*, interseminal scale tissues.

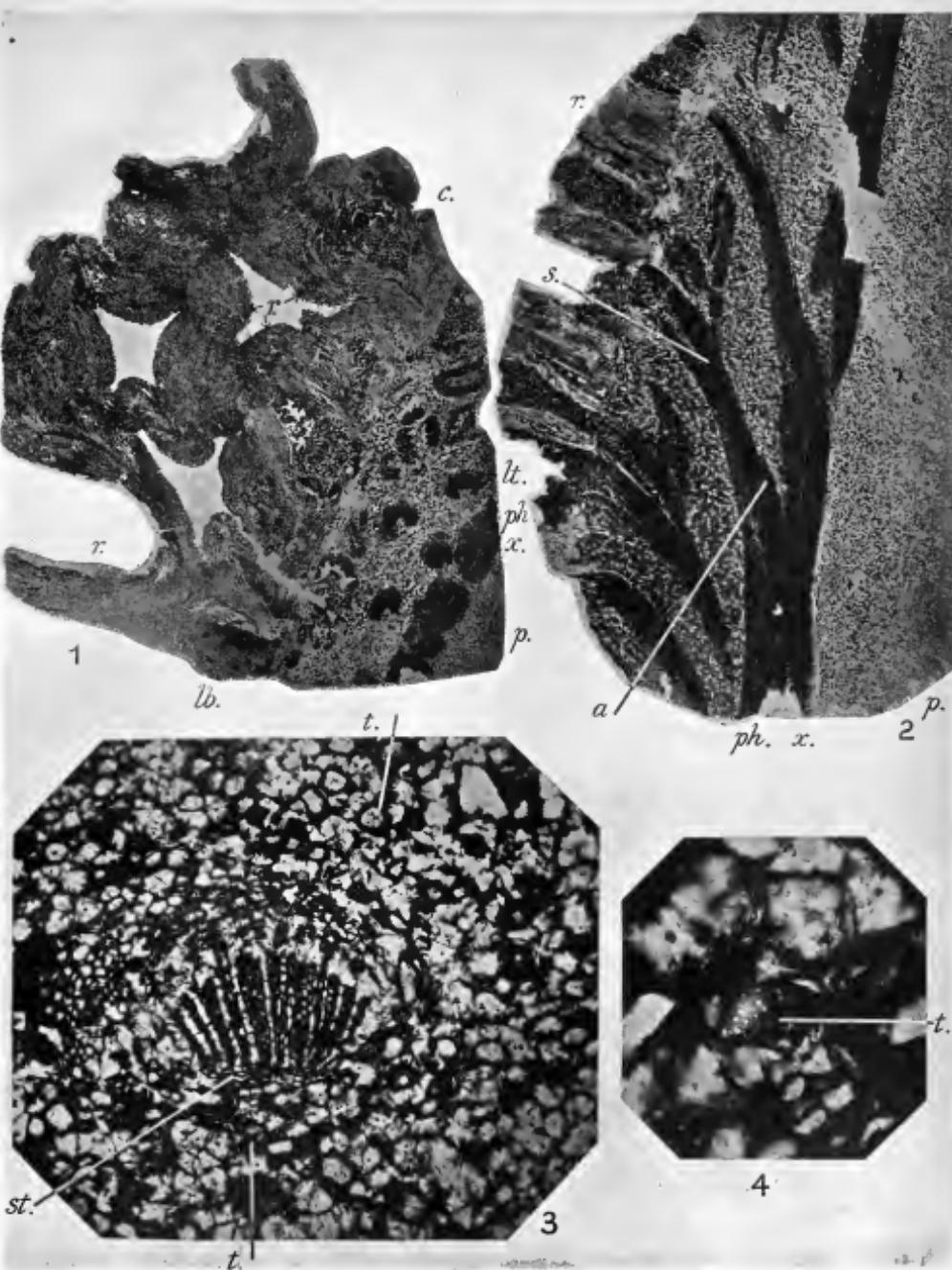


PLATE 23.

Bennettites maximus, CARR.

Fig. 1.—Transverse section of a part of the main trunk, showing the central vascular cylinder with outgoing leaf-traces, and the large areas of ramenta surrounding the young cones and leaf-bases: *p.*, pith; *x.*, xylem of central cylinder, the white streak running tangentially separates it from the phloem, *ph.*; *lb.*, leaf-base, cut somewhat obliquely; *lt.*, leaf-trace; *c.*, obliquely cut cone, surrounded by its scales cut in various directions; *r.*, ramenta. (Sect. No. 28293. \times about $1\frac{1}{2}$ diam.)

Fig. 2.—Radial longitudinal section of trunk corresponding to transverse Section 1. Lettering the same as above. Note particularly the outgoing strand *a.*, and the way it breaks up in a spraying manner to several strands almost simultaneously at *s.* This should be compared with text-fig. 18. (Section No. 28291. \times about $1\frac{1}{2}$ diam.)

Fig. 3.—Transverse section of the ground-tissue and a vascular bundle of a leaf-base. Note the thick-walled, pitted cells of the bundle sheath all round the vascular strand *st.*, and the larger cells of the same type thickly scattered through the ground tissue *t.* Compare with text-fig. 21.

Fig. 4.—Small portion of ground tissue as in fig. 3, enlarged to show the pitted transmutation elements *t.* Note that the pits are in definite areas.

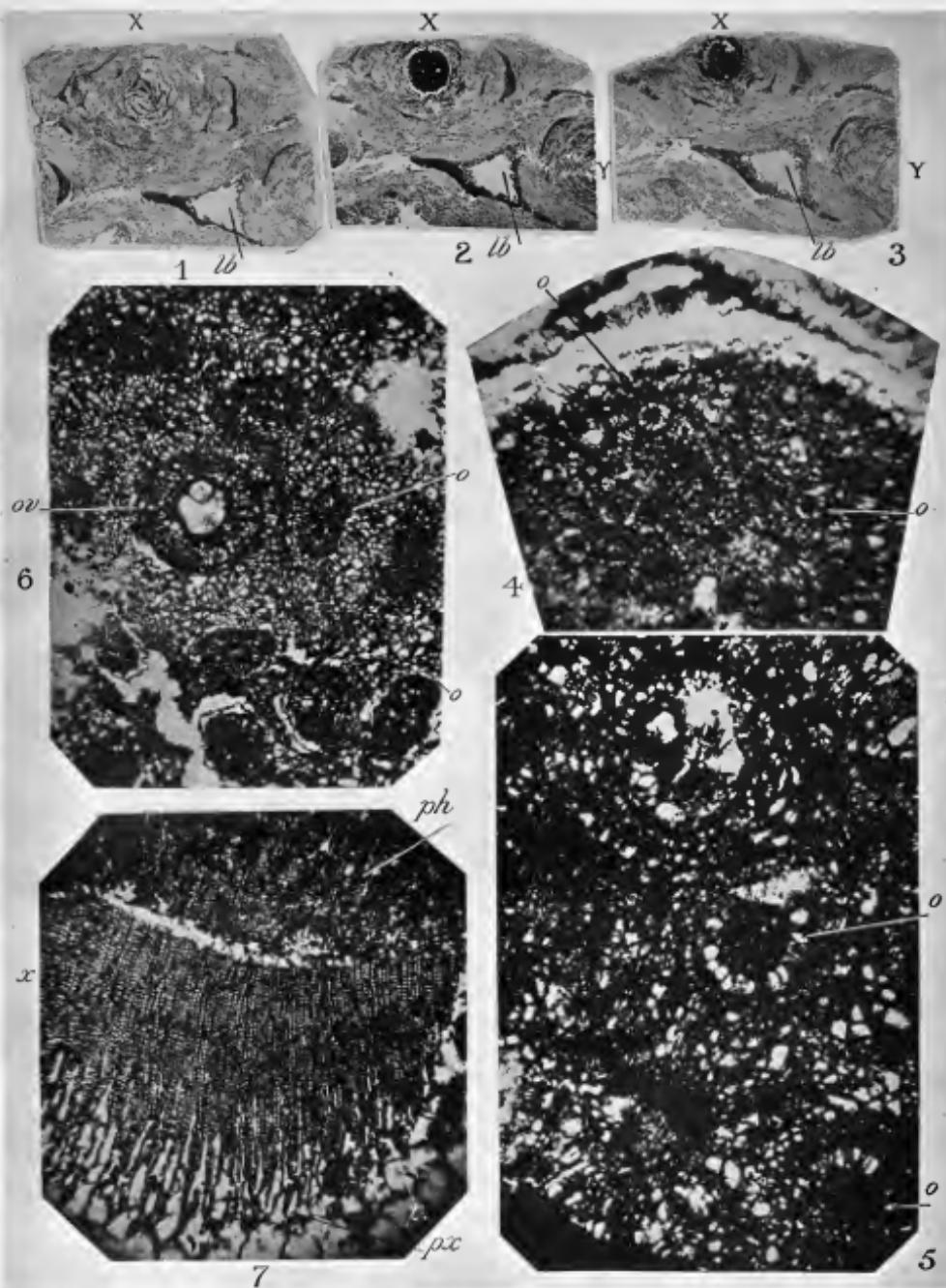


PLATE 24.

Figs. 1, 2 and 3 almost magnified 1·5 diameters.

Fig. 1.—Transverse section of the top of Cone X with surrounding ramenta, leaf-base *lb*, and parts of other cones and leaf-bases. [Slide 28296.]

Fig. 2.—Cone X cut in the ovulate region. Note the dense meristematic tissues. On the right the scales of Cone Y are seen. [Slide 28298.]

Fig. 3.—Cone X cut in region of γ disc. Cone Y seen on the right. [Slide 28299.]

Fig. 4.—The edge of Cone X further enlarged, showing the developing ovules *o*. [Slide 28297.]

Fig. 5.—Another portion of the same further magnified; *o*, ovules, in which the limiting layer and the solid central mass can be distinguished. [Slide 28297.]

Fig. 6.—Central portion of the same cone section as shown in figs. 4 and 5, showing a central ovule more developed than the others, *ov*. It is surrounded by a number of other, less perfect ones, *o*.

Fig. 7.—Portion of the vascular cylinder of the main axis: *p*, pith; *px*, protoxylem; *x*, centrifugal xylem; *ph*, phloem. [Slide 28298.]